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Area Effects and Visual Selection in Cepaea nemoralis (L.) and Cepaea hortensis

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STUDIES ON *CEPAEA*

II. AREA EFFECTS AND VISUAL SELECTION IN *CEPAEA NEMORALIS* (L.) AND *CEPAEA HORTENSIS*

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CONTENTS

The snails *Cepaea nemoralis* and *C. hortensis* show an extensive and stable polymorphism involving the colour and banding pattern of the shell. The surveys on the Berkshire Downs, the Purbeck Hills and part of lowland Somerset reported here show, together with previous ones, that both species can occur in lowland and chalk upland localities, but the distribution of the two species in any one locality is different. This difference may be related to topography as on the Berkshire Downs and

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the Purbecks, or to habitat as in south-east Somerset. There are no regional differences in the *C. nemoralis* polymorphism, most morphs so far recognized being present in every locality. The colour polymorphism in *C. hortensis* is much more extensive in the southern localities than in those from central England and there are alo regional differences in the banding polymorphism.

Two types of morph frequency variation occur in both species. The first described was variation with habitat, the second, variation related to geographical position. The surveys show that habitat variation occurs in both lowland and upland areas, although it does not necessarily occur in either. Thus both species show morph frequency variation with habitat round Oxford and on the eastern Berkshire Downs. Only *C. hortensis* shows such variation on the Purbeck Hills although *C. nemoralis* is present there. The evidence, although not conclusive, indicates that neither species shows habitat variation in lowland south-east Somerset, but there is good evidence that neither species shows such variation on the western Berkshire Downs, the Marlborough Downs or Salisbury Plain.

The morphs showing frequency variation with habitat are not always the same in either species. Round Oxford, and on the eastern Berkshire Downs, brown, pink and banded *C. nemoralis* with at least the upper two bands missing, are at a high frequency in woods, and yellows and bandeds are at a high frequency in other habitats. *C. hortensis*, on the other hand, shows variation in the frequency of fused bands and yellow effectively unbandeds between habitats in these two localities. On the central Berkshire Downs, spread banded show habitat variation together with other morphs in *C. nemoralis*. On the Purbeck Hills where pinks, browns and unbandeds are common in *C. hortensis* the habitat variation is very similar to that of *C. nemoralis* round Oxford.

Habitat variation is not restricted to strikingly different morphs. Different types of pink *C. nemoralis* show such variation on the Berkshire Downs, and fusions of the upper or more bands in *C. hortensis* also show variation there.

All the variation of morph frequency described above is best explained on the hypothesis of visual selection.

Morph frequency variations related to geography give rise to large areas of stable morph frequency irrespective of habitat, the so-called area effects. The surveys to date indicate that area effects are restricted in both species to upland localities. The Berkshire Downs survey of *C. nemoralis* shows that area effects and habitat variation are not mutually exclusive. In different localities, related on an east/west axis, most morphs may show habitat variation, some show habitat variation and some area effects, or most show area effects.

Area effects may occur in both species in the same locality as on the western Berkshire Downs, where the limits of the various area effects in the two species are semi-coincidental, or they may only occur in one species, *C. nemoralis*, on the Purbeck Hills.

There is no experimental evidence as to the cause of area effects but there is some evidence from the present surveys which supports Cain & Currey's (1963*a*, *c*) suggestion that they are maintained by selection.

I. Introduction

Populations of the polymorphic land snails *Cepaea nemoralis* and *C. hortensis* are known to be widespread in the more calcareous habitats in England (Taylor 1914). Samples that have been taken from some of these populations show two phenomena, variation of morph frequency with habitat and area effects.

Cain & Sheppard (1954), working mainly in the Oxford district, and Currey, Arnold & Carter (1964), working in south Warwickshire, have shown that in these two lowland districts of central England much of the variation of the shell colour and banding patterns of *C. nemoralis* is correlated with the background of the habitats in which the populations occur, and they suggested that this correlation is due to visual selection. Sheppard (1951) and Arnold (1966) have shown that the selective agent causing much of this variation of morph frequency with habitat is selective visual predation by the song thrush, *Turdus ericetorum*. Murray (1962) has shown that small mammals also predate the snails selectively,

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but here the selection as suggested by Cain (1953) is probably by tone and not by colour.

Clarke (1960), working mainly round Oxford, has shown that the morph frequencies of *C. hortensis*, a species closely related to *C. nemoralis*, also vary with habitat. As in *C. nemoralis* the most cryptic morph is at a high frequency in any given habitat, but the method by which this crypsis is achieved is different in the two species. Thus brown and/or pink effectively unbanded morphs are at a high frequency in samples of *C. nemoralis* taken from woods, whereas yellow five bandeds are common in samples taken from more open habitats (hedgerows, rough herbage, etc.).

Colour morphs other than yellow are relatively rare in *C. hortensis* in the Oxford district, but samples from woods contain a high proportion of yellow-banded shells with fused bands, which are effectively dark. Samples of *C. hortensis* from more open habitats contain a lower proportion of banded shells with fused bands, and often have a high proportion of yellow unbanded ones.

Cain & Currey (1963*a*, *b*), working on high rather exposed chalk downland, have obtained different results from those above. On the Marlborough Downs they found (1963*a*) that the morph frequencies of *C. nemoralis* remained more or less constant over large areas regardless of the habitats from which the samples were taken, and in spite of visual selection. Cain & Currey have defined these large areas of stable morph frequency as area effects. In a further survey of part of Salisbury Plain, a high chalk plateau to the south-west of the Marlborough Downs (1963*b*) they found area effects in *C. nemoralis* and also in *C. hortensis*.

The areas of constancy of morph frequencies are of the order of several square miles, whereas the size of the panmictic unit of the snails has been shown by Lamotte (1950) and Murray (1962) to be about 60 m in diameter. Cain & Currey (1963*a*, *c*) have argued for this and other reasons, that the area effects cannot be due to random genetic drift past or present, and are most likely to be caused by selection.

This paper describes three surveys of populations of *C. nemoralis* and *C. hortensis*. The first was carried out on the Berkshire Downs, a region of chalk downland chosen because of its geographical position between the Oxford district and the Marlborough Downs. The other two surveys were carried out in the south-west of England, one in a lowland district, similar topographically to the Oxford and south Warwickshire districts, and the other on a high chalk ridge in Dorset close to the sea. These two areas were chosen for comparison with previous surveys, all of which had been made in central England.

II. Methods

1. *Collecting*

Some 300 random samples of *C. nemoralis* and 200 samples of *C. hortensis* were collected from a variety of habitats on the Berkshire Downs over an area of approximately 40 km by 10 km. Previous workers' data (Cain & Currey 1963*a*; Clarke 1960, 1962) from various parts of the region have also been used.

During 1962 and 1963 random samples of *C. nemoralis* and *C. hortensis* were collected from a variety of habitats on the Purbeck Hills in Dorset. Samples of *C. hortensis* were collected from hedgerows and roadside verges in south Somerset by Captain C. Diver in

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1921 and 1922 and he very kindly let me have the sample scores. Samples of *C. hortensis* and *C. nemoralis* were collected from woods in this region in 1963.

Individual samples were taken from as small an area as possible and within an area corresponding to the size of the panmictic unit in the case of most live samples. Visual predation by birds and/or small mammals occurs extensively over all regions, and samples of predated snails were collected only when it was likely that the shells came from a single habitat type. Sheppard (1951) has shown that thrushes do not carry snails far if anvils are plentiful. Sheppard's (1951) and Cain & Sheppard's (1954) results suggest that selection by thrushes is of the order of 1% and this sort of error is unlikely seriously to affect the results of a general survey.

During sampling a careful search was made to ensure that the less conspicuous morphs were not overlooked. Clarke (1962) showed that successive samples of one species taken by different workers did not differ from each other significantly. Resampling of a few populations originally sampled by Cain & Currey (1963*a*) shows no significant variation in colour, and significant variation in banding in only two comparisons (table 7)*.

2. *Scoring*

Shells were scored for age (adult, juvenile), and colour and banding following Cain & Sheppard (1954), Cain & Currey (1963*b*) and Clarke (1960). The scores of colour and banding for each sample are shown in tables 1 to 6. Juveniles were not included in the scores of samples of more than 21 adult individuals and not at all in samples from mixed colonies of the two species.

All colour and banding morphs previously described (Cain & Sheppard 1954; Cain & Currey 1963*a*, *b*; Clarke 1960, 1962) occur in these regions. Spread bandeds in which the band pigment spreads more or less diffusely into the interband part of the shell occur at quite high frequencies in *C. nemoralis* over parts of the Berkshire Downs and Purbecks, particularly where mid-bandeds are at a high frequency. Cain, King & Sheppard (1960) showed that spread bandedness is controlled by a major gene, but it is not yet known to what extent the degree of spread bandedness is genetically based. Spread bandeds have, however, been divided into two classes, heavy spread in which the band pigment spreads densely and evenly over the shell, and light spread in which the pigment is diffuse and only much nearer the lip with only a slight darkening effect.

Samples of *C. hortensis* from the Berkshire Downs show great variation in band pigmentation from normal dark brown pigment to its complete absence. Murray (1963) has shown that there are three major allelic genes controlling the degree of pigmentation which produce dark pigment, pale pigment and no pigment. Samples from the wild show a wide range of pale pigment from rather dark to very pale, but the degree of pigmentation has been classed following Murray (table 2).

III. GENETICS

Cain *et al.* (1960) described a gene for spreading of band pigment in *C. nemoralis* and showed that it is dominant to its allele. They also showed that the locus is linked to the colour locus. Samples of *C. nemoralis* collected from the Purbecks suggest that there may

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* The tables are gathered as an Appendix commencing on p. 427.

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be at least one other locus controlling the spreading of band pigment. The phenotype is distinct from band fusion and does not show much variation. It therefore seems likely that it is controlled by a major gene. Table 3 shows that spread bandeds are restricted largely to five banded individuals. There are only two spread mid-bandeds in two of the 21 samples with spread bandeds. Mid-bandeds are rare and therefore only those samples in which the expected number of spread mid-bandeds is greater than one have been analysed statistically. In all nine such samples the actual number of spread mid-bandeds is zero which is a significant deficiency ($p = \frac{1}{2}^{9}$). In all samples with more than one colour class spread bandeds are distributed randomly with respect to colour and there is therefore no evidence of linkage between these two loci.

The nearly complete deficiency of spread mid-bandeds suggests epistasis or interference between the two loci and, together with the lack of evidence of linkage, it suggests that the spread banded gene on the Purbecks is at a different locus to that described by Cain *et al.*

IV. Habitats

Both *C. nemoralis* and *C. hortensis* occur in several different habitat types in the various regions. The range of habitats is similar to that found by Cain & Sheppard (1954) and Cain & Currey (1963 *a*, *b*) and their classification was used namely, grassland, rough herbage, nettles in grass, hedgerows, beech woods and mixed deciduous woods.

Cain & Sheppard pointed out that there was greater diversity within their open habitat classes than within the woodland classes. There is considerable variation in both the open habitats and woods in the regions discussed in this paper, but there are no significant differences in morph frequency in samples from either the different open habitats or the woods in any one area. As the open habitats are more similar with regard to background than any of them are to woods, only the two broad habitat classes have been used in most analyses.

V. Survey I. The Berkshire Downs

1. *Description of the region investigated*

(*a*) *Physiography and geology*

The Berkshire Downs form a high chalk plateau running east/west for about 40 km, connected in the east to the Chiltern Hills and in the south-west to the Marlborough Downs. The plateau dips gently to the south-east and is dissected by valleys of streams flowing south and east into the River Thames. To the north the chalk forms an escarpment rising from the Jurassic plain below, It runs east/west along most of its length but in the west it turns south-west to the Marlborough Downs. In the east and west there is a relatively narrow lower chalk step but in the centre of the region the escarpment rises steeply through 400 ft. Along its length and from the north, the escarpment is cut into by a number of dry valleys. In the east these run north/south, are steep sided and are sheltered from the prevailing south-westerly winds. There are few in the centre of the region but in the west they run north-west/south-east.

The region investigated has been arbitrarily defined. It is limited in the east, except for a few samples beyond it by the valley of the River Thames which cuts through the chalk plateau more or less at right angles to the escarpment. The limit in the west is a wide valley that now contains a small stream, the River Og which separates the Berkshire from the

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Marlborough Downs. The northern limit is the bottom of the escarpment, and the southern one the lower valley of the Lambourn stream and a continuation of its line east and west.

(*b*) *Vegetation*

Much of the vegetation has until recently been grassland, probably for several thousand years (Tansley 1939). The original woods were cleared by man starting in the Neolithic and thereafter grazing by sheep and cattle prevented any extensive reafforestation (cf. Colquhoun & Morley 1941). The only extensive ploughing of the downs in the historical past was probably during the Napoleonic Wars and also in the 1870s (Jones in Cain & Currey 1963 *a*), but it seems unlikely that even then habitats available to *Cepaea* were so reduced that random genetic drift played an important part in determining morph frequencies in either species. Since the last war ploughing has been extensive and habitats suitable for *Cepaea* are restricted to the few woods, verges of tracks crossing the Downs, areas too steep for the plough and racehorse training gallops.

The woods in the east of the region are the largest and probably the oldest (Tansley 1939). Most of the woods are stands of pure beech and are planted, although some may be quite old (Cain & Currey 1963 *a*). They can be divided into two types, those in the valleys with a well-developed herb and shrub layer and those on the high plateau which are very open and have few herbs and shrubs.

Rough herbage, a mixture of grasses and dicotyledons, is one of the most common habitats for *Cepaea* on the downs.

2. *Distribution of* C. nemoralis *and* C. hortensis (figure 1)

C. nemoralis is widespread in all habitats. It is common both in the valleys and on the more exposed parts of the high plateau. It is, however, absent in the south-east and a few other places where the chalk is capped by clay with flints. In the east of the region the species is found on the escarpment and on the lower chalk plain but in the west it is mostly absent from either.

C. hortensis is also widespread in all habitats but in the east is limited to the bottoms of valleys and to woods on the high plateau. It does not occur on the escarpments in the east. In the west, however, it is very common on the escarpment and where this is low extends over the top and for a short way on to the high plateau. Elsewhere on the plateau it is restricted to valley bottoms and woods as in the east.

3. *Morph frequencies in* Cepaea nemoralis

(*a*) *Delimitation of districts*

Figures 2 and 3 show the frequencies of the yellow, pink and brown morphs and the unbanded, mid-banded and five-banded morphs in all the samples collected. There are considerable differences in the frequencies of the various morphs over the region which can therefore be divided into several districts. The delimitation of these districts is to some extent arbitrary as there are no physical barriers, and the morph frequencies change regularly from those characteristic of one district to those of the next. It is convenient to distinguish districts with characteristic morph frequencies and those which show a change of morph frequency from east to west. The districts so defined are, from east to west:

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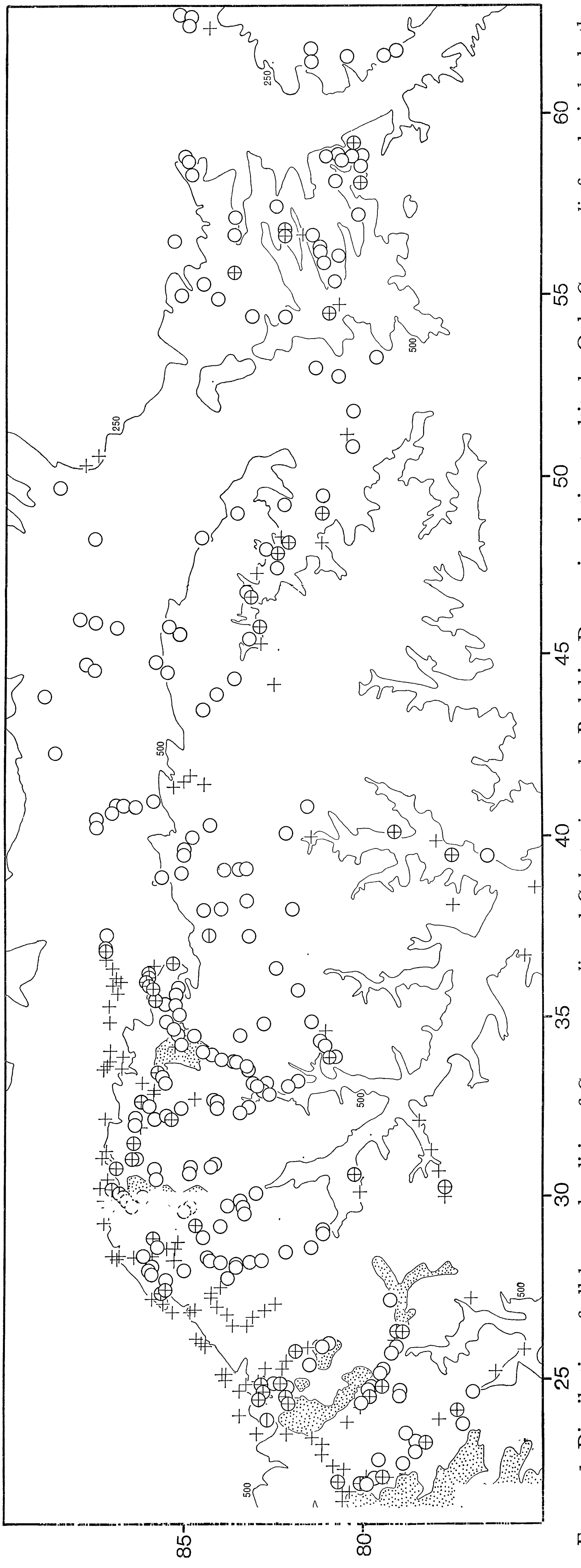

FIGURE 1. Distribution of all known localities of *Cepaea nemoralis* and *C. hortensis* on the Berkshire Downs, in relation to altitude. Only *C. nemoralis* found, circle; both species found, circle with cross; *C. hortensis* only found, cross. Contours at 250 ft. intervals, and over 750 ft. stippled. Five km squares of the National Grid shown.

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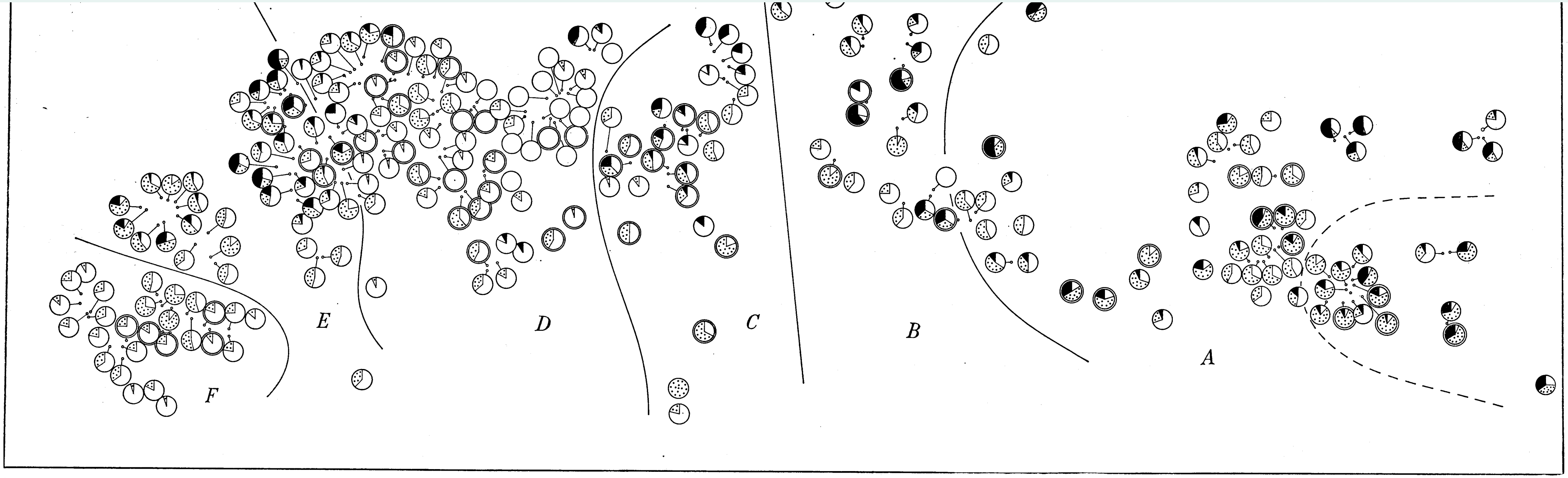

FIGURE 2. Proportions of brown (black), pink (stippled) and yellow (white) shells of *C. nemoralis* in the Berkshire Downs. Samples from woods represented by double circles; samples from open habitats, single circles. The centre of each circle is at the point of collection except where the circle is displaced for clarity, in which case it is joined to a small circle showing the collecting point. Districts: *A*, Goring; *B*, Ilsley; *C*, Wantage; *D*, Lambourn; *E*, Uffington; *F*, Liddington. Broken line encloses area effect in district *A*.

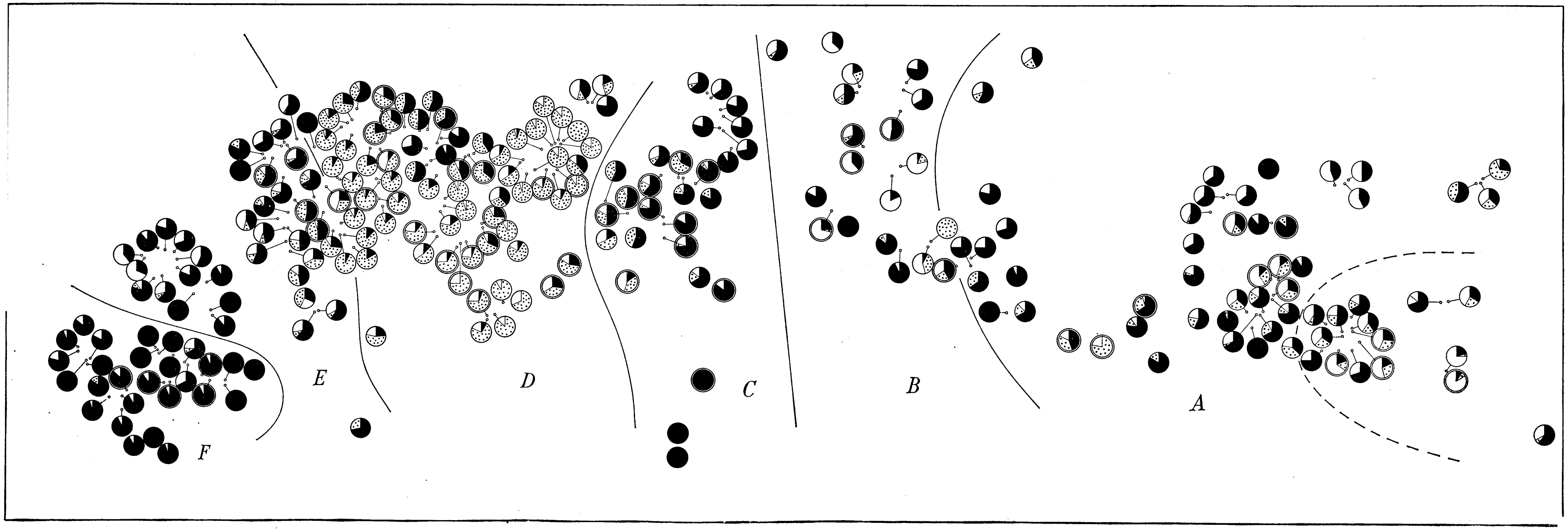

FIGURE 3. Proportions of five-banded (black), mid-banded (stippled) and unbanded (white) shells of *C. nemoralis* on the Berkshire Downs. Symbols as in figure 2.

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Goring, Ilsley, Wantage (intermediate), Lambourn, Uffington (intermediate) and Liddington. The Goring district is nearest to the part of Oxfordshire where Cain & Sheppard worked and the Liddington district in the west is separated from the Marlborough Downs only by the valley containing the River Og.

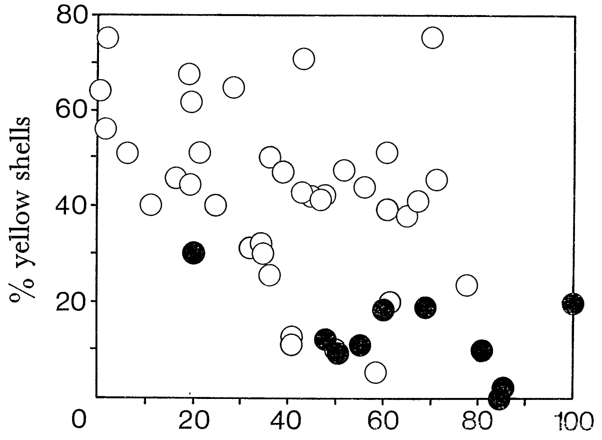

FIGURE 4

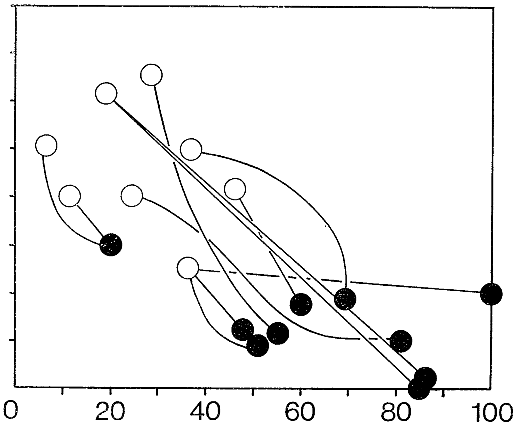

FIGURE 5

FIGURE 4. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat for samples of *C. nemoralis* from localities in the Goring district except those in the immediate vicinity of Goring on Thames. Woods, black circles; open habitats, open circles.

FIGURE 5. Scatter diagram comparing the frequencies of yellow and effectively unbanded shells in pairs of samples from Goring district. The woodland and open habitat symbols of each pair are joined.

(*b*) *Goring district*

Over most of this district there is variation of shell colour and banding with habitat not geography. Figure 4 gives the appropriate scatter diagram. Testing the median separation of the symbols for woods against open habitats on the effectively unbanded axis gives a $\chi^2_{(1)}$ of 6·18, $P < 0{\cdot}025$. A similar test on the yellow axis gives a $\chi^2_{(1)}$ of 10·2 $P < 0{\cdot}01$. As the measurements on each axis are independent the Chi squareds can be summed giving a probability of $P < 0{\cdot}001$. Woods therefore contain significantly more non-yellow effectively unbandeds than open habitats. The woods are not confined to one geographical area and a comparison of pairs of samples from woods and their nearest open habitats (never separated by more than 1 km) is shown in figure 5. Seven of the woods are less yellow and more effectively unbanded than their adjacent open habitats $(p = \frac{1}{4}^{7})$.

These results agree remarkably well with those obtained by Cain & Sheppard (1954) from the Oxford district and Currey, Arnold & Carter (1964) for south Warwickshire. These workers argued that differences in morph frequencies in samples of *C. nemoralis* from different habitats were due to selective visual predation. Sheppard (1951) and Arnold (1966) have shown that thrushes predate snails selectively the most cryptic morph being favoured. Lamotte (1959) has also shown that yellow unbandeds are more resistant than other morphs to extremes of temperature and he suggested that yellow unbandeds are favoured for this reason in more exposed open habitats, whereas in woods with less extreme conditions pinks and bandeds are more likely to be found. His explanation holds

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for colour in the samples from this district discussed above, but not for banding. The hypothesis of visual selection, on the other hand, accounts for the distribution of both colour and banding and it therefore seems more likely that this is the selective mechanism operating.

There is a geographically distinct group of samples in the south-east corner of the district in the immediate vicinity of Goring on Thames and on either side of the river. The samples from both woods and open habitats have high proportions of pinks and browns. As a geographical group these samples indicate an area effect. Figure 6 is the appropriate scatter diagram and shows that although pinks and browns are at a high frequency samples from woods have the higher proportion of effectively unbandeds, although not significantly so at the 5% level. This variation could be accounted for on the hypothesis of visual selection.

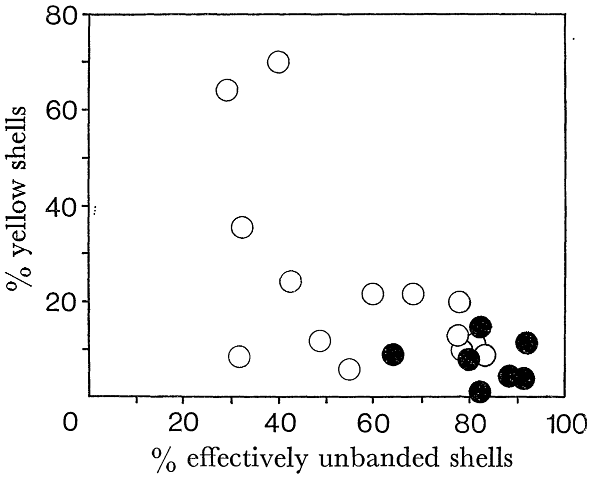

FIGURE 6. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat for samples of *C. nemoralis* from localities in the immediate vicinity of Goring on Thames.

Cain *et al.* (1960) have shown that there are at least two alleles for the shade of pink, linked to the banding locus. Three pink shades can be distinguished in samples from this district, the first two corresponding to Cain *et al.*'s dark pink and pale pink, the latter having an orange flush. The third is very pale pink and is almost certainly genetically determined. Depth of pink can only be scored with any certainty in unbandeds and mid-bandeds because five-bandeds are usually fascialbate. This condition is thought to be genetically determined and produces a white opaque layer on either side of the band. In five-bandeds it fills the interband region and pales the shell ground colour. The proportions of dark and very pale pinks have been compared in all possible samples (table 8). The woodland samples from the pink area effect contain a significantly higher proportion of dark pinks than the open habitats ($P < 0{\cdot}01$). The frequency difference of the very pale pinks is not significant, although several open habitats have a high proportion of this morph. In the area where visual selection predominates the woods tend to have a higher proportion of dark pinks and a lower proportion of very pale pinks than the open habitats, although neither of these differences is quite significant at the 5% level because of two

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exceptional woods. As both groups of samples show the same trends they have been lumped (figure 7). Median tests on this larger group of samples reach significance on both the dark pink and very pale pink axes ($P < 0.01$ in both cases).

Dark pinks are more like the colour of beech litter than very pale pinks which are rather straw coloured. As the woods here are mostly pure beech the high frequency of dark pinks may be due to visual selection. Very pale pinks may be at a visual advantage against the dead grass in the tussocks on the chalk grassland.

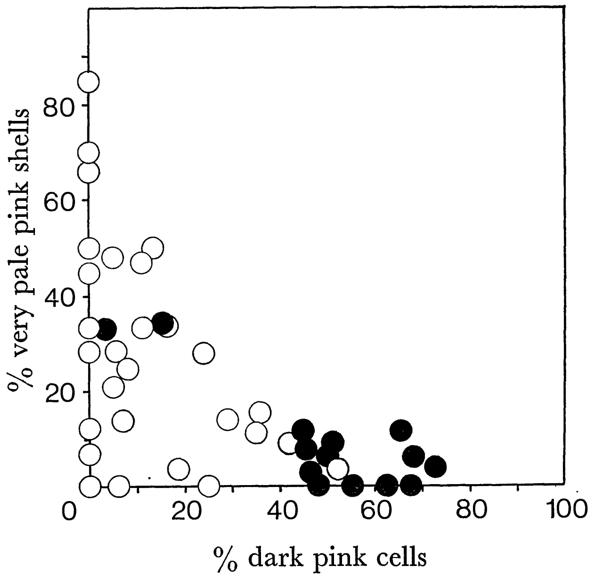

FIGURE 7. Scatter diagram for percentage dark pink shells, very pale pink shells, and habitat for samples of *C. nemoralis* from localities in Goring district.

Median tests on the frequency of yellows in samples in the pink area effect show no significant difference between samples on either side of the river which is 80 ft. wide at this point and must be a barrier to snails. Goodhart (1962) showed that active snails drown after $1\frac{1}{2}$ h in water and although inactive snails are known to survive longer periods of immersion they would be carried downstream by the river. The samples in this area effect are almost opposite each other on either side of the river and it is therefore unlikely that their similarity can be due to gene flow. These observations support Cain & Currey's (1963*c*) arguments against Goodhart (1963) in that samples on either side of a barrier, showing similar gene frequencies are unlikely to have differently coadapted genotypes. The morph distribution is unlikely to be a relict one as the populations are up on the sides of a fairly narrow valley in which the course of the Thames is unlikely to have changed much over a considerable period.

Mid-bandeds are at a relatively low frequency but are at a higher frequency in woods than in open habitats (figures 3 and 13*b*). Unbandeds have a similar distribution except in those few open habitat samples which contain browns all of which are unbanded. Previous work has shown that there often appears to be interference between brown and banding (Lamotte 1954; Cain & Sheppard 1957; Cain *et al.* 1960; Clarke & Murray 1962*a*). Such interference would account for finding only brown unbandeds in this district.

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Clarke (1960) found that many banded *C. hortensis* had fused bands in woods. He suggested that such fusions darkened the shell and were cryptic. He grouped all fusion types but observation of active snails suggests that fusion of the upper two bands of the shell or all the bands has a greater darkening effect than fusion of only the lower two bands. Banded individuals of *C. nemoralis* have consequently been grouped into three classes, no fusions, fusion of the upper two or more bands and fusion of only the lower two bands. There is no difference in frequency of either of the fusion classes with habitat in either the area effect or visual selection area. Different results were obtained from a similar analysis of *C. hortensis* data from this district (see below, p. 418).

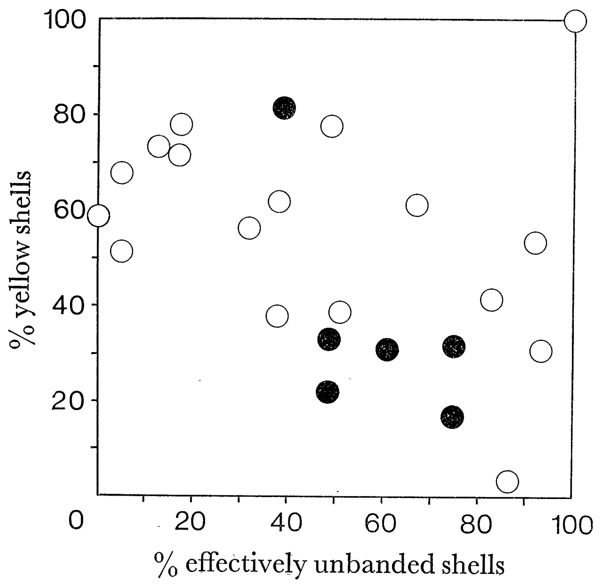

FIGURE 8. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat for samples of *C. nemoralis* from localities in Ilsley district.

(*c*) *Ilsley district* (figure 8)

Samples are separated on their morph frequencies into easterly and westerly groups. The six samples from the east indicate a small effectively unbanded area effect. The samples from the west show habitat variation similar to that in the Goring district with the exception of one woodland sample. Two pairs of samples from woodland and open habitats separated by less than 400 yards show considerable habitat variation.

		per cent yellow	per cent effectively unbanded
SU 439841	wood	17	75
SU 435845	open habitat	78	17
SU 459869	wood	23	49
SU 460876	open habitat	64	38

There is no indication of a higher proportion of fusions in woods nor a correlation of either class of fusion with habitat. There are not sufficient samples to carry out a useful analysis of pink frequency variation.

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(*d*) *Wantage district* (figure 9)

The scatter of symbols is different from the two previous districts, most woods having a higher proportion of yellows. Within the district most open habitats have a higher proportion of yellows than the woods. Samples were not collected from adjacent woods and open habitats but a comparison of 10 pairs separated by up to a kilometre shows a higher proportion of yellows in seven open habitats. The frequency of the effectively unbanded morphs varies considerably in both the woods and open habitats, but tends to be low in both habitat types in the east and increases in both in the west. This is largely due to an increase in the frequency of mid-bandeds westwards. In woods this increase is through 60% over 5 km.

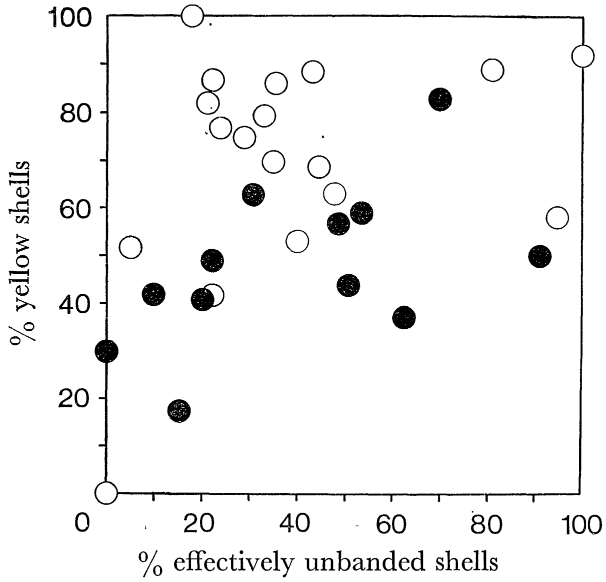

FIGURE 9. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat for samples of *C. nemoralis* from localities in Wantage district.

There is no variation of fusions with habitat. Analysis of the frequency of pinks was not possible as many of the samples were of old predated shells.

(*e*) *Lambourn district*

Cain & Currey (1963*a*) originally collected samples from this district. They pointed out that morph frequencies were similar to those in district A on the Marlborough Downs and showed a considerable area effect for mid-bandeds. Further samples confirm this and show that the area effect is extensive on the high plateau in the north as well as in the valleys in the south (figure 10, which includes Cain & Currey's samples).

Five-bandeds occur in most samples at a low frequency but reach higher frequencies in the north-west, in one case as high as 90%. Unbandeds occur sporadically but are never at a higher frequency than 30%.

Browns occur very rarely and at a low frequency (figure 2). Pinks occur in several samples and may be at a high frequency in some, particularly in the valley area in the south. Cain & Currey (1963*a*) showed that pinks were at a higher frequency in woods than in open habitats in a southern valley and suggested that visual selection for colour

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was effective there. Further sampling in the south shows similar variation. Most of the woodland samples from the high plateau in the north have a lower frequency of pinks than might be expected on the hypothesis of visual selection considering the nature of their background. Three wood samples, however, contain a high frequency of pinks, much higher than open habitats close by. One such sample comes from the southern end of a long wood where it is sheltered by rising ground in the west. The sample from the northern end of this wood on top of the escarpment contains few pinks and is similar in this respect, to an open habitat close by. The other two anomalous samples come from woods on top of the escarpment which are not apparently sheltered. Other woods in similar positions contain populations with very low pink frequencies.

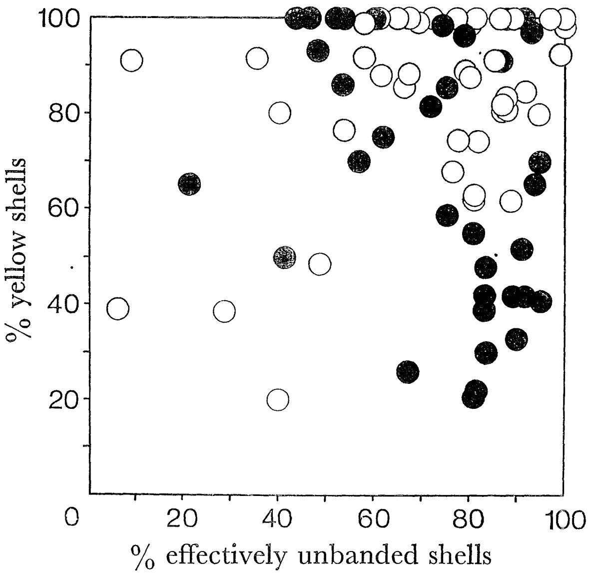

FIGURE 10. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat for samples of *C. nemoralis* from localities in Lambourn district.

Yellows are at a high frequency in most samples on the high plateau and are the only colour morphs present in several samples particularly a group in the north-east.

Analysis of the three shades of pink showed no variation with habitat. Pale pinks are by far the most common in all habitats.

Cain & Currey (1963*a*) reported that spread bands occur frequently on the Lambourn Downs. Further sampling has confirmed this and it is only here that they are present in nearly every sample and are at a high frequency in some. Analysis shows that spread bandeds are not randomly distributed with respect to colour. Of the 30 samples which contain more than 10 pink and 10 yellow shells, 29 show an excess of yellow spread bands (table 1) ($\chi^2_{(1)} = 26$, $P < 0{\cdot}001$). This excess occurs in both woods and open habitats. These findings are in agreement with those of Cain *et al.* (1960) who showed linkage between spread bands and colour. They also indicate that yellow spread bands are at an advantage here. A *t* test of samples with more than 50 shells shows that spread bands are not as common in yellows in woods as they are in open habitats. ($t_{(62)} = 7{\cdot}8$ $P < 0{\cdot}001$; woods $\bar{x} = 21\,\%$, open habitats $\bar{x} = 28\,\%$). There are, however, differences in the amount to which the band pigment spreads (p. 400) and analysis shows (table 9) that heavy spread

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bands are at an excess in 18 of 22 samples from woods but in only 17 of the 34 samples from open habitats. In the absence of selection an equal number of samples should show an excess and deficiency of heavily spread bands. Although this is true of open habitats the woods differ significantly from this expectation ($\chi^2_{(1)} = 8{\cdot}8$ $P < 0{\cdot}01$).

There is no correlation of fusion with habitat but this is not surprising as banded individuals are mostly rare and fused bandeds are very rare.

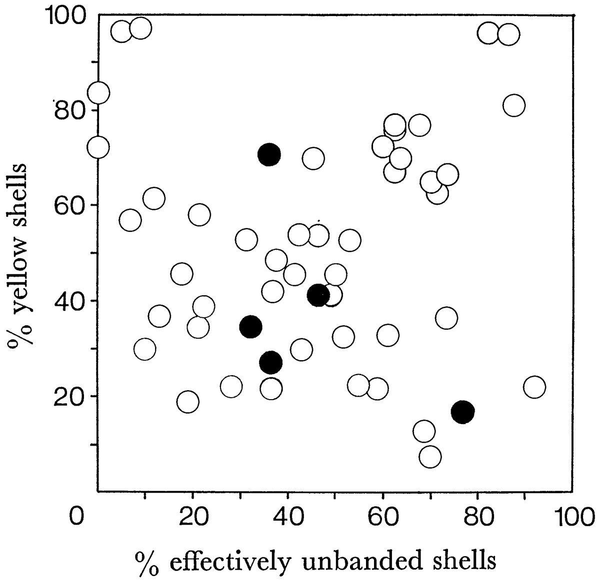

FIGURE 11. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat for samples of *C. nemoralis* from Uffington district.

In order to investigate the effects of visual selection Cain & Sheppard (1954) grouped genetically different but visually similar morphs. Using their group (figure 10) only some samples show morph frequencies consistent with the visual properties of the habitat background, since there are area effects for high frequency of mid-bandeds and yellows in most samples. Using similar criteria to Cain & Sheppard's a group of dark shells can be distinguished including browns, pinks, yellow heavy spread mid-bandeds and yellow bandeds with fused bands (table 10). A comparison shows that such dark morphs are at a higher frequency in woods than in open habitats ($\chi^2_{(1)} = 4{\cdot}97$, $P < 0{\cdot}05$). Of 16 pairs of samples from woods and open habitats separated by less than 600 yards, 13 woods have a higher proportion of dark morphs ($\chi^2_{(1)} = 6{\cdot}2$, $P < 0{\cdot}02$). This sort of variation with habitat is very similar to that found in *C. hortensis* round Oxford (Carter 1967). It therefore seems that in both these species the type of variation with habitat depends on the morphs available (see also p. 420).

(*f*) *Uffington district* (figure 11)

Mid-bandeds are at a high frequency in the east close to the Lambourn area effect, but they are replaced south-westwards across the district in all habitats by five-bandeds. There is an area effect for browns which show no consistent variation with habitat. There is considerable variation in the frequency of pinks and yellows.

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The five woodland samples contain a lower proportion of yellows than their nearest open habitats (table 11), but four of the woods have a rather high proportion of yellows considering the nature of their background. Three woods have a higher frequency of effectively unbandeds than adjacent open habitats but only one wood has a high frequency of these morphs.

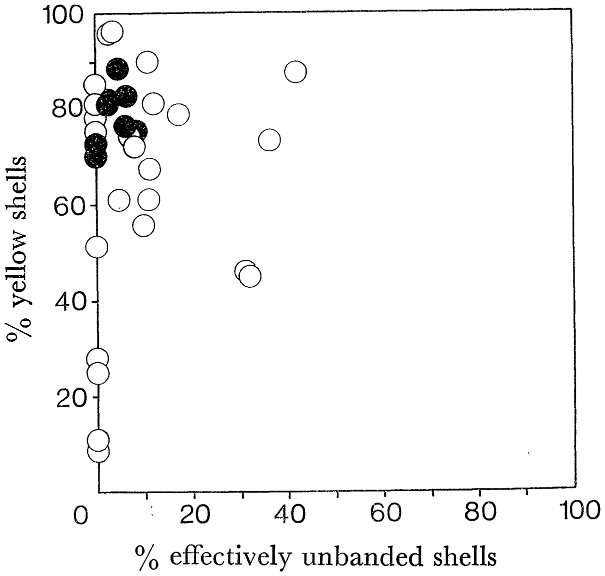

Figure 12. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat for samples of *C. nemoralis* from Liddington district.

(*g*) *Liddington district* (figure 12)

There is an area effect for five-bandeds which are at a very high frequency in all habitats and are the only banding types present in many samples. There is considerable variation in the frequency of yellows, but no regular variation with habitat. There is a higher proportion of fusions in open habitats than in woods ($P < 0\cdot05$), and although it is not significant at the 5% level of probability there is a positive regression of lower band fusions on upper band fusions ($y = 5\cdot6+0\cdot399x$, $P < 0\cdot1 > 0\cdot05$). This is the only district with any correlation of fusions with habitat and it is in the wrong direction on the hypothesis of visual selection. Sedlmair (1956) reported that on transfer of yellow unbanded and yellow five-banded heavily fused *C. hortensis* from a hot bright dry environment to a cold dark damp one, the bandeds were most active. This could be some sort of black body effect and might explain the distributions of fusions in *C. nemoralis* here.

(*h*) *Marlborough Downs* (Cain & Currey 1963*a*)

These downs lie some 5 km to the west of the Liddington Downs and are separated from them by a wide valley now containing the River Og. The few collections from this valley contain, with one exception taken from rising ground, only *C. hortensis*. The single *C. nemoralis* sample has 72% five-bandeds. There is a five-banded area effect in *C. nemoralis* on that part of the Marlborough Downs nearest to Liddington. To the south and west of this area effect morph frequencies change rapidly and over most of the Marlborough Downs there is a strong area effect for effectively unbanded morphs, mid-bandeds being the only banded morph in most samples.

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There is no evidence of morph frequency variation with habitat in any except a few topographically distinct samples. These few exceptional samples were taken from some woods in a southern valley (cf. the Lambourn Downs). They have a high frequency of pinks and Cain & Currey argued that this could be because of visual selection.

4. *The distribution of browns on the Berkshire Downs*

Analysis of the distribution of browns shows that in all six districts there are relatively more samples containing browns on the escarpment and lower chalk shelf than on the high chalk plateau (table 12). The actual difference is significant only in the Liddington district, but the similarity of trend in all six districts is significant ($P < 0.05$).

In two series of samples collected from the escarpment in the Wantage district and a third in the Lambourn district browns are at a higher frequency in the lower samples than in the top-most ones. Browns do not, however, always occur on the escarpment as is shown by several samples in the Lambourn district and other scattered ones. Cain & Currey (1963*a*) suggested that the distribution of browns might be related to climate since browns occur more often on those parts of the Marlborough Downs where cold air accumulates. The distribution of browns on the Berkshire Downs supports this interpretation since cold air does build up from the bottom of steep slopes (personal observation, and Gieger 1959).

5. *Distribution of pinks and yellows on the Berkshire Downs*

In the east the variation in frequency of these morphs is primarily with habit, but their distributions west of Lambourn suggest that they may be affected by climate. Sedlmair (1956) showed that pinks prefer rather lower temperatures than yellows (17 °C against 20 °C) and Lamotte (1959) has shown that yellows are most resistant to extremes of temperature. The distribution of the two morphs on the western Berkshire Downs agrees with these experimental results. In all three western districts pinks occur mainly in valley bottoms and at the bottom of gentle slopes in open habitats. They also occur in woods. This distribution is very similar to that of *C. hortensis* and overlaps the distribution of browns. The lower lying localities are probably cooler than the higher flatter ones because of the ponding of cool air (Geiger 1959). I have seen and felt such ponding on the escarpment in the early morning when snails were active.

The temperature changes on the high flat plateau are probably greater than in valleys and on the northern escarpment. It is on the high plateau that yellow *C. nemoralis* are common and these are the morphs most resistant to extremes of temperature.

6. *Comparison of gene frequencies*

Figure 13 shows all the samples from the Berkshire Downs in relation to their east/west position and compares the frequencies of the yellow, unbanded and mid-banded genes calculated on Hardy Weinberg assumptions. There are considerable differences between the frequency of the yellow gene in woods and open habitats in the east, but this difference gradually disappears westward. The gene is fixed in several samples from the eastern Lambourn Downs (centre of figure) but from there westward there is considerable variation although this is not by habitat. Both un- and mid-banded gene frequencies are higher in

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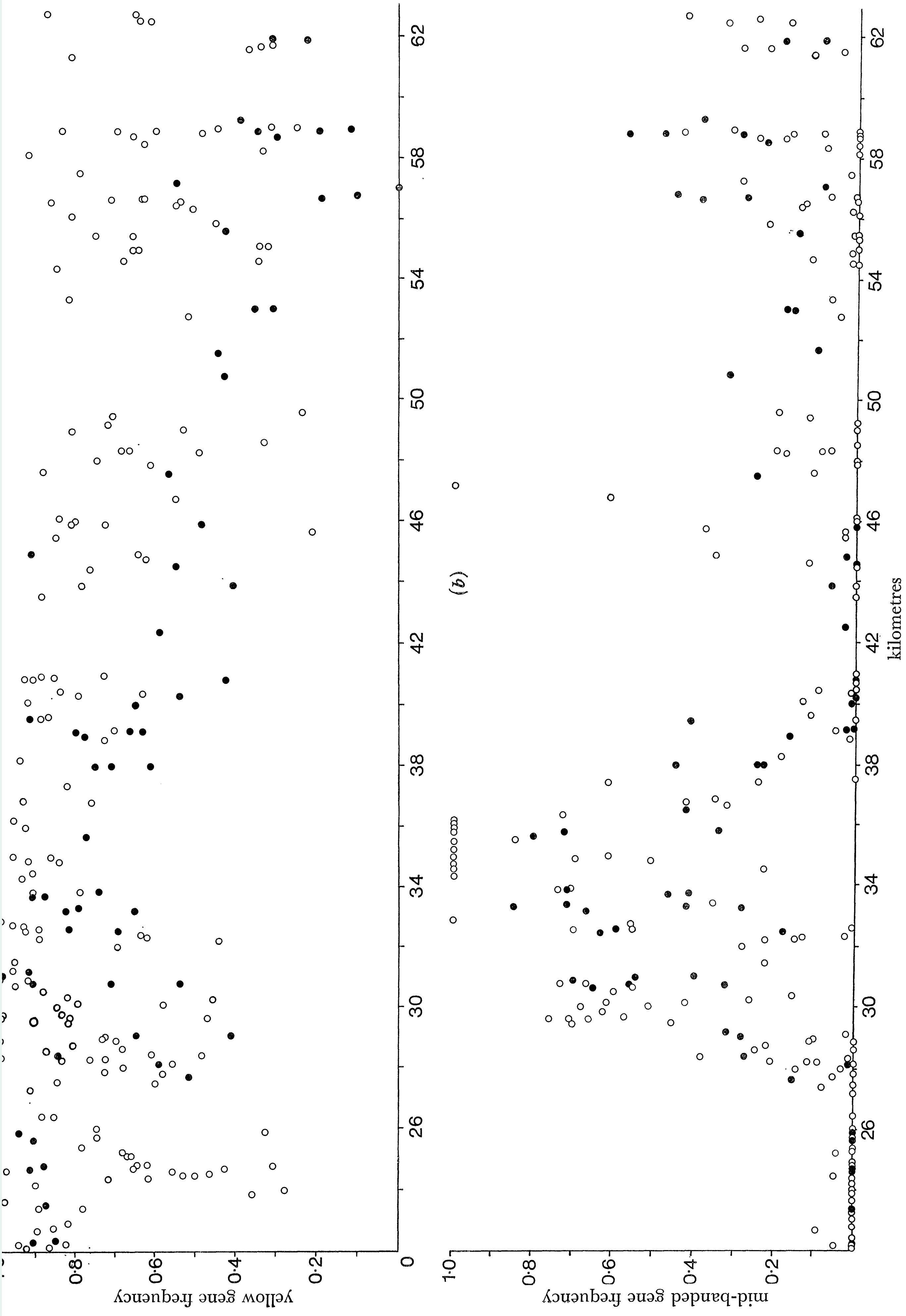

FIGURE 13 (*a*) and (*b*). For legend see facing page.

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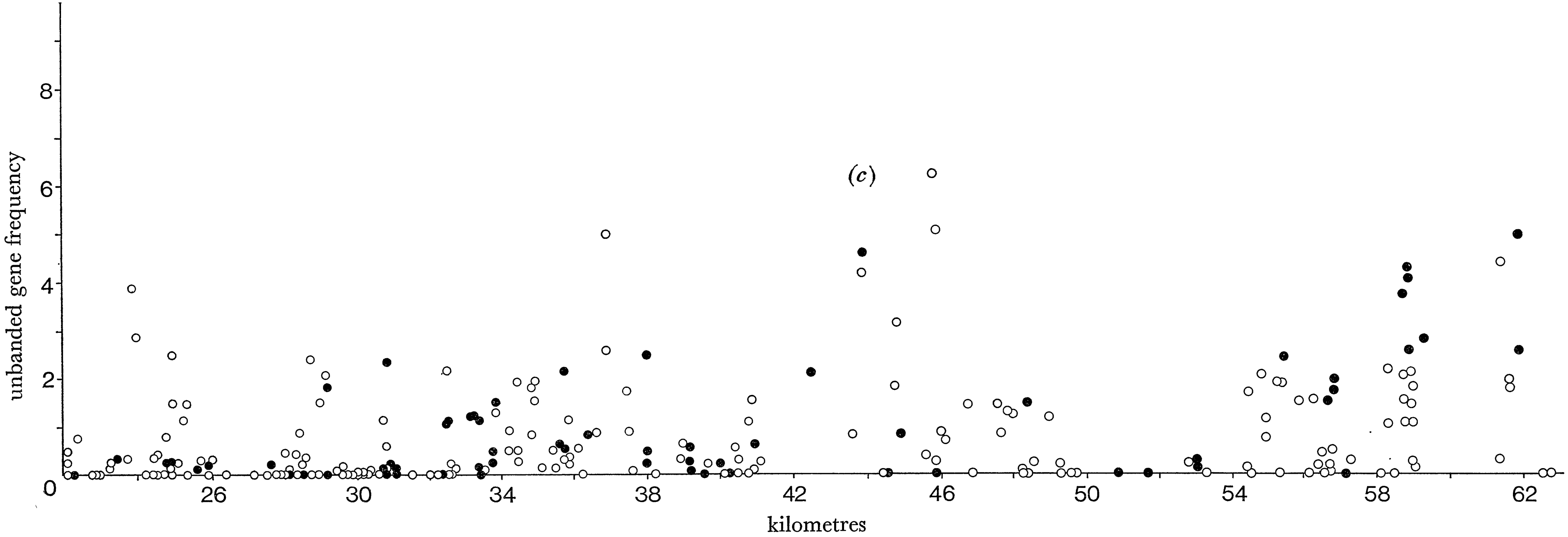

FIGURE 13. A comparison of the frequency of : (*a*) the yellow gene, (*b*) the mid-banded gene, and (*c*) the unbanded gene in populations of *C. nemoralis* in woods and open habitats on the Berkshire Downs. The gene frequency is shown on the ordinate. The abscissa represents the east/west distance in kilometres. Samples from woods, black circles; samples from open habitats, open circles.

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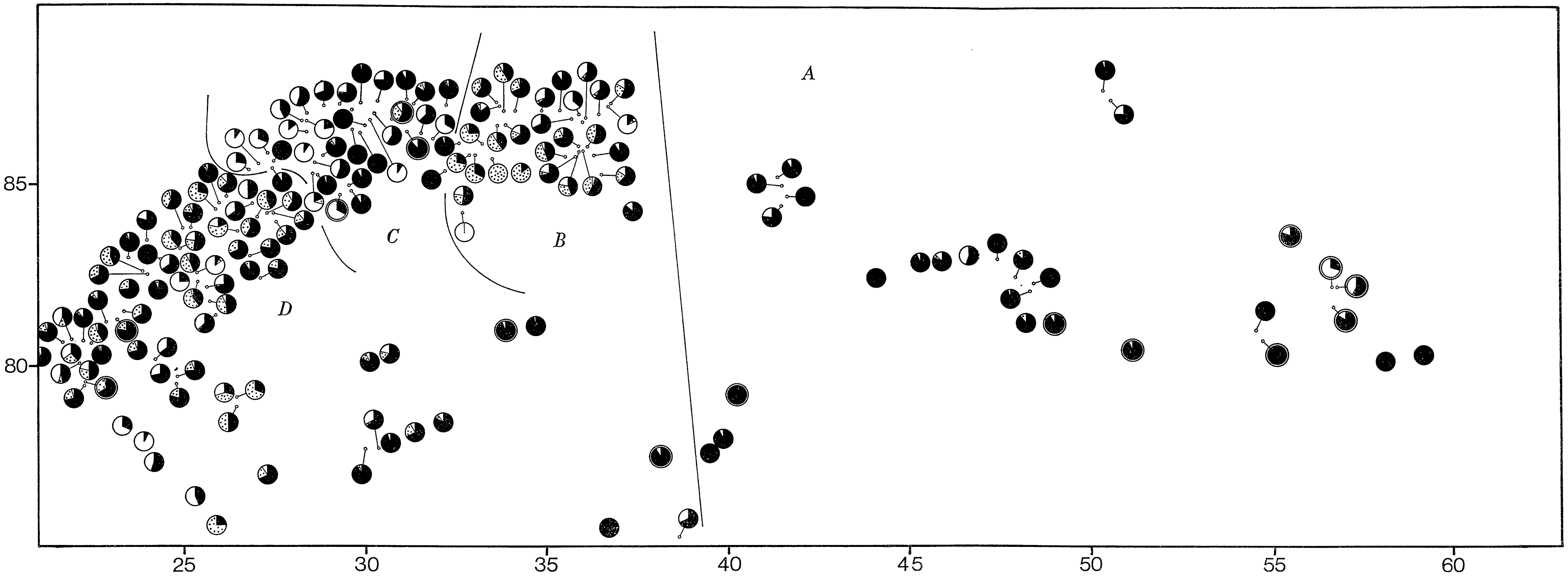

FIGURE 14. Proportions of five-banded (black) hyalozonate (stippled) and unbanded (white) shells of *C. hortensis* on the Berkshire Downs. Woods represented by double circles, samples from open habitats by single circles. The centre of each circle is at the point of collection except where the circle is displaced for clarity, in which case it is joined to a small circle showing the collecting point. Districts: *A*, Goring, Ilsley and Wantage; *B*, Lambourn; *C*, Uffington; *D*, Liddington.

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woods than in open habitats in the east. The mid-banded gene frequency rises sharply in the centre of the region giving rise to the Lambourn area effect. It drops off again in the west in the Liddington area effect. The unbanded gene is at a generally low frequency from Lambourn westward. There is no relationship between the frequency of the mid- and unbanded genes from Lambourn westwards.

7. *Summary*

Birds, particularly the Song Thrush, *Turdus ericetorum*, are known to predate *C. nemoralis* and anvils are common over the whole of the Berkshire Downs suggesting that such predation is widespread. Morph frequency variation with habitat is greatest, and similar to that round Oxford, on the east of the downs. In the west variation is largely related to geography and topography. This suggests that visual selection is effective in the east but is largely outweighed in the west.

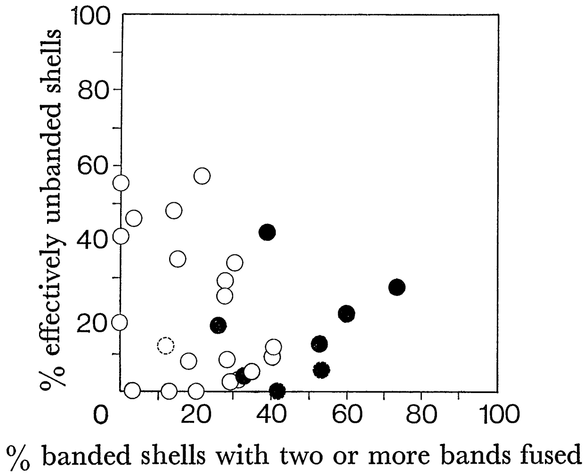

FIGURE 15. Scatter diagram for percentage yellow effectively unbanded shells, percentage banded shells showing fusions of two or more bands, and habitat for samples of *C. hortensis* from localities in Goring, Ilsley and Wantage districts.

8. *Morph frequencies in* C. hortensis (figure 14)

Yellows are the most common colour morph on the Berkshire Downs. Browns occur sporadically and at a low frequency. Pinks are absent. Five-bandeds are the most common banding morph. Unbandeds are present. Dark-banded, pale-banded and hyalozonate individuals also occur. The frequencies of the different banding morphs are different in different parts of the region.

(*a*) *Goring, Ilsley and Wantage districts*

There are rather few samples of *C. hortensis* in these three districts in comparison with *C. nemoralis*. The morph frequencies in samples from each habitat type do not differ significantly over the whole area and therefore they have all been considered together. Figure 15 compares the frequency of yellow effectively unbandeds and bandeds with fused bands in all samples following Clarke (1962). Woods have significantly more bandeds with fused bands than open habitats ($P < 0{\cdot}05$) as would be expected on the hypothesis

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of visual selection. There is no such significant difference in the frequency of yellow effectively unbandeds.

Lang (1904) and Murray (1963) have some evidence that fusion of bands is multifactorially controlled. Samples from woods in these three districts have a significantly higher proportion of bandeds with their upper or more bands fused than those from open habitats ($P < 0{\cdot}01$). There are no significant differences in the proportions of fused lower bands.

(*b*) *Lambourn, Uffington and Liddington districts* (figure 14)

C. hortensis is very common in all these three districts but in none of them is there any indication of morph frequency variation with habitat that would suggest the action of visual selection. Five-bandeds with dark bands and pale bands occur in all three districts. There are three main area effects, one in each district, characterized on the absence or low frequency of either the unbanded or hyalozonate morph. All three area effects have similar limits to those in *C. nemoralis* except that they are displaced slightly to the north because of the rather different distribution of the two species (p. 402). In the Lambourn district unbandeds are mostly at a low frequency, whereas hyalozonates are mostly at a higher frequency. This is therefore an area effect for hyalozonates. In the Uffington district hyalozonates are absent in all but three samples, whereas unbandeds occur commonly. This is therefore an area effect for unbandeds. In the Liddington districts both hyalozonates and unbandeds occur but more samples show a high frequency of hyalozonate so that this is also an area effect for hyalozonates. None of these area effects is as clear cut as those in *C. nemoralis* as there is some variation between samples within each of them.

Pale bandeds are common in the three districts. There is a significant positive regression of pale bandeds on hyalozonates in the Liddington district ($P < 0{\cdot}05$) and a nonsignificant one in the Lambourn district. Clarke (1962) found that open habitat samples with a low frequency of yellow effectively unbandeds often had a high frequency of pale bandeds and he suggested that these might be selected for visually. If pale bandeds are included with effectively unbandeds in the Berkshire Downs samples then there is an increase in the proportion of the 'pale morphs' in both woods and open habitats. This suggests that the positive correlation between pale bandeds and hyalozonates here is not due to visual selection.

VI. SURVEY II. THE PURBECK HILLS

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

The Purbeck Hills between Swanage and Weymouth are formed by chalk and limestone outcroppings isolated to the south by the sea and along most of their length to the north by more acid Quaternary deposits. In the east the chalk forms a high ridge running east/west and rising sharply from the Quaternary deposits to the north. To the south is the sea. All the samples of *C. nemoralis* and several samples of *C. hortensis* were collected from this ridge. In the west the chalk spreads to the north and forms a more undulating plateau. Samples collected from this part of the region contained only *C. hortensis*. Both species

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were found in a variety of habitats. In the west *C. hortensis* occurs on the high plateau but in the centre and east it is mostly confined to the lowest part of the ridge being replaced on the higher parts by *C. nemoralis*.

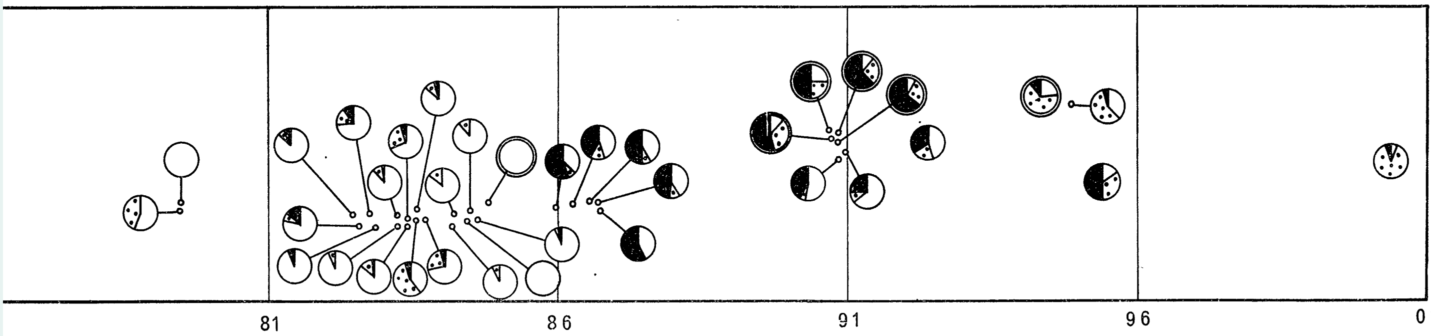

FIGURE 16. Proportions of brown (black), pink (stippled) and yellow (white) shells of *C. nemoralis*, on the Purbeck Hills. Samples from woods represented by double circles; samples from open habitats by single circles. The centre of each circle is at the point of collection except where the circle is displaced for clarity, in which case it is joined to a small circle showing the collecting point.

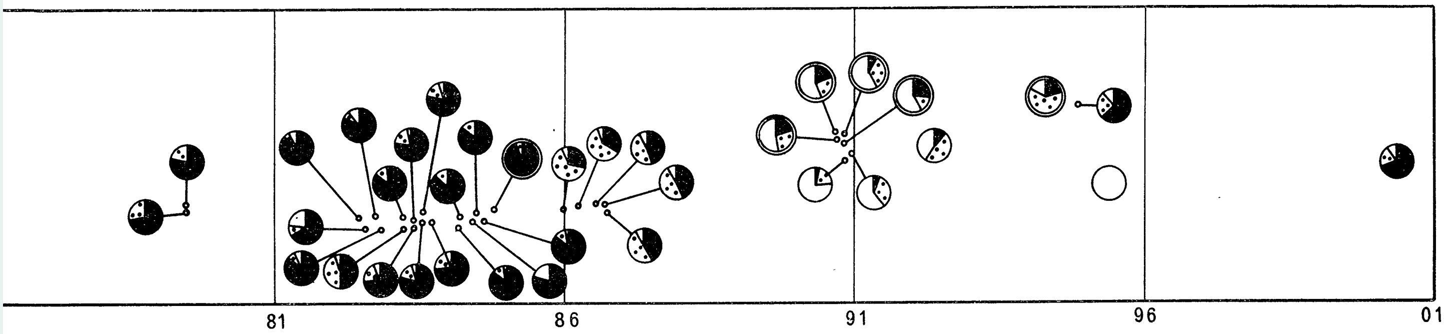

FIGURE 17. Proportions of five-banded (black), mid-banded (stippled) and unbanded (white) shells of *C. nemoralis* on the Purbeck Hills.

2. *Morph frequencies in* C. nemoralis (figures 16, 17)

Area effects for colour and banding occur in this species in this region. The westernmost samples show an area effect for high frequency of yellow five-bandeds. Pinks although always at a rather low frequency are at their highest frequency in the centre of this area effect. There are no consistent differences in the frequencies of any morph between the seaward and landward sides of the ridge. The morph frequencies in the only woodland sample are very similar to those in an adjacent open habitat sample, although the wood is well established and a large number of bird predated shells were found in it.

In the central group of samples there is an area effect for browns. Although the ridge is continuous here there is an unsampled gap dividing the samples into two subgroups. This part of the region is in the East Lulworth Artillery Range and difficulties over access have prevented further sampling. Both subgroups show a high frequency of browns in all habitats, but the westerly samples have a high frequency of mid-bandeds, the easterly ones have a high frequency of unbandeds. Several of the browns collected were banded, a situation not often previously found in *C. nemoralis* (see p. 407). The samples collected

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from a large wood on the landward side of the ridge have a higher frequency of non-yellow morphs than samples from open habitats close by on the top of the ridge. There is very little difference in the frequency of the effectively unbandeds but most open habitats have the higher frequencies of these morphs.

The four samples taken from the eastern end of the ridge have fewer browns than those in the central group and possibly come from a pink area effect.

3. *Morph frequencies in* C. hortensis

There are no signs of area effects in this region in contra-distinction to *C. nemoralis*. The species is polymorphic for both colour and banding unlike most of the Oxford district and the Berkshire Downs. Figure 18 is a scatter diagram comparing the proportions of yellow and effectively unbandeds for all the samples of *C. hortensis* collected. This shows a separation very much like, but not as great as, that found in *C. nemoralis* in areas where visual selection is effective. The median separation on the yellow axis is significant ($\chi^2_{(1)} = 9{\cdot}9$, $P < 0{\cdot}01$), but that on the effectively unbanded axis is not ($\chi^2_{(1)} = 1{\cdot}1$, $P > 0{\cdot}05$). Comparing 10 pairs of samples from woods and open habitats within 600 yards of each other (figure 19) shows that nine woods contain more yellows and seven woods fewer bandeds than their respective open habitats. The probability that only three of ten pairs of samples do not agree with the hypothesis of visual selection for both colour and banding is 0·0198. There is therefore good evidence that visual selection is effective in this species in this region. The variation in morph frequency found, although common in *C. nemoralis* populations where visual selection is effective, has not been described in *C. hortensis* before.

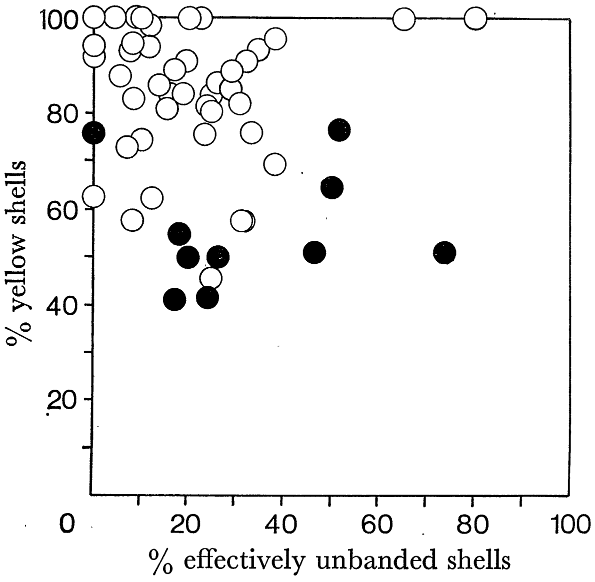

FIGURE 18. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells and habitat for samples of *C. hortensis* from localities on the Purbeck Hills.

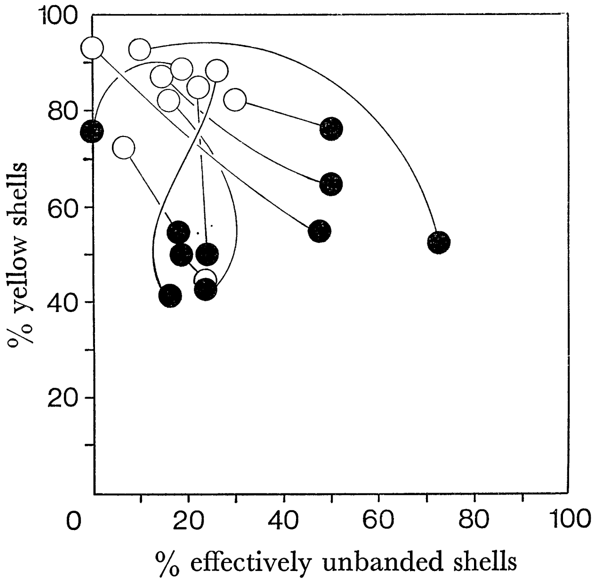

FIGURE 19. Scatter diagram comparing the frequencies of yellow and effectively unbanded shells in pairs of samples of *C. hortensis* taken from the Purbeck Hills. The woodland and open habitat symbols of each pair are joined.

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VII. SURVEY III. SOUTH-EAST SOMERSET

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

The part of Somerset investigated lies between the towns Castle Cary and Wincanton. It is relatively low lying (between 200 and 500 ft.) with rolling country side. The whole region is given over to agriculture and the only habitats available to *Cepaea* are the roadside verges, hedgerows and woods which are mainly mixed deciduous. The region is much more like the Oxford district than either of the other regions discussed in this paper.

In 1921 and 1922 Diver collected samples only from hedgerows and roadside verges and these contained only *C. hortensis* with one exception. My samples from woods contained *C. nemoralis* as well as *C. hortensis*, but the samples from open habitats collected as close as possible to Diver's original sites, plus a few others, contained with two exceptions only *C. hortensis*. The two exceptional samples were taken from very thick and overgrown hedgerows (almost small copses). This distribution of the two species in relation to habitat differs from that round Oxford (except in the east of that region) but agrees with a previous workers' findings (Clarke in Cain & Currey 1963*a*) that where one species is common the other is confined to woods.

2. *Morph frequencies in* C. nemoralis (table 5)

Pinks and browns are the most common colour morphs and effectively unbanded are at a high frequency in these samples. These frequencies agree with the nature of the woodland background on the hypothesis of visual selection, but as there are no samples from open habitats for comparison it is not possible to determine whether or not visual selection is effective.

3. *Morph frequencies in* C. hortensis (table 6)

Most samples contain browns and/or pinks and both five-bandeds and unbandeds occur as on the Purbecks. Five-bandeds are at a high and rather constant frequency and there is a regional preponderance of this morph. There are no other morph frequency regularities. There are no area effects within the district, nor is there any variation of either colour or banding morphs (including band fusions) with habitat. A great deal more information is required before the processes affecting these populations can be ascertained.

VIII. DISCUSSION

The morph frequency variation with habitat in populations of *C. nemoralis* and *C. hortensis* reported here is such that it is best explained on the hypothesis of visual selection. Such selection has been shown to occur in several experiments (Sheppard 1951; Arnold 1966). The present surveys add to previous ones (Cain & Sheppard 1954; Cain & Currey 1963*a*, *b*; Currey *et al.* 1964; Clarke 1960) and show that this sort of variation with habitat is not restricted, in either species, to one type of locality as seemed the case previously. It occurs on both lowland plains round Oxford and in south Warwickshire and on the high chalk of the eastern Berkshire Downs and the Purbeck Hills. It does not necessarily occur in either type of locality however, as has been shown by surveys of the Marlborough Downs, Salisbury Plain, western Berkshire Downs and part of lowland south-east Somerset.

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In some localities such as round Oxford and on the eastern Berkshire Downs both *C. nemoralis* and *C. hortensis* show morph frequency variation with habitat. There is one locality, the Purbeck Hills, where although both species are present, only *C. hortensis* shows such variation. In several localities including the Marlborough Downs, Salisbury Plain and western Berkshire Downs both species are present but neither show this sort of variation.

Previous surveys indicated that *C. nemoralis* showed the same sort of morph frequency variation with habitats in different localities and this was always different from that shown by *C. hortensis* (Clarke 1960). The present surveys show that neither of these observations hold. On the eastern Berkshire Downs, as around Oxford, pink, brown and banded *C. nemoralis* with at least the upper two bands missing are common in woods, whereas yellows and five-bandeds are more frequent in other habitats. In the centre of the Berkshire Downs near Lambourn, these differences are less marked because mid-bandeds and yellows are mostly at a high frequency in all habitats. Spread-bandeds are present in many of these samples and it has been shown (p. 410) that if yellow spread bandeds are grouped with certain other morphs then woods contain a higher proportion of these 'dark' morphs than open habitats.

Clarke (1960) found that pinks and browns were rare in samples of *C. hortensis* from round Oxford but he showed that there was habitat variation in the frequency of yellow unbandeds and bandeds with at least two bands fused, woods containing a higher proportion of the effectively dark morphs. There is habitat variation in the frequency of band fusions in samples of this species taken from the Berkshire Downs but on the Purbeck Hills the species shows quite different habitat variation. Pinks and browns are relatively common there as are unbandeds, and these morphs show variation with habitat that is similar to that found in *C. nemoralis* round Oxford.

In *C. nemoralis* it appears to be involvement of particular morphs in local area effects which limits morph frequency variation with habitat. There is no evidence of regional differences in the polymorphism in this species whereas in *C. hortensis* there are marked differences associated with locality and region. Data on the shell colour polymorphism of *C. hortensis* are shown in table 13. Comparisons of the occurrence of pinks and browns in the samples from different localities are given below and show that the colour polymorphism is more extensive in two lowland localities from different regions than their nearest chalk uplands, although not quite significantly so in one comparison. There is a great increase in the number of populations containing colours other than yellow in the localities from the south-east, south and south-west in comparison with the Oxford district and Berkshire Downs which are more central.

Lowlands compared to nearest chalk upland

Oxford: Berkshire Downs $\chi^2_{(1)} = 13{\cdot}6,\ P < 0{\cdot}05$
Somerset: Purbeck Hills $\chi^2_{(1)} = 3{\cdot}1,\ P > 0{\cdot}05$

Lowlands comparison

Oxford district: Somerset $\chi^2_{(1)} = 10{\cdot}3,\ P < 0{\cdot}05$
Oxford district: Kent $\chi^2_{(1)} = 13{\cdot}9,\ P < 0{\cdot}05$

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Chalk upland comparison

Berkshire Downs: Marlborough Downs	$\chi^2_{(1)} = 0{\cdot}5,\ P > 0{\cdot}05$
Berkshire Downs: Salisbury Plain	$\chi^2_{(1)} = 6{\cdot}9,\ P < 0{\cdot}05$
Berkshire Downs: Purbecks	$\chi^2_{(1)} = 62{\cdot}0 < 0{\cdot}05$
Berkshire Downs: South Downs	$\chi^2_{(1)} = 21{\cdot}6,\ P < 0{\cdot}05$
Marlborough Downs: Salisbury Plain	$\chi^2_{(1)} = 0{\cdot}7,\ P > 0{\cdot}05$
Marlborough Downs: Purbeck Hills	$\chi^2_{(1)} = 18{\cdot}7,\ P < 0{\cdot}05$
Marlborough Downs: South Downs	$\chi^2_{(1)} = 5{\cdot}3,\ P < 0{\cdot}05$

The comparison of samples from different chalk downland localities shows that those closer together are more similar with respect to the colour polymorphism than those which are more distant.

Comparison of tables 2 and 4 shows that hyalozonates occur locally quite frequently in *C. hortensis* populations on the Berkshire Downs, whereas they are absent on the Purbeck Hills.

Data from the survey of *C. nemoralis* on the Berkshire Downs show that gene and morph frequency variation with habitat is not equally great in all populations. There is a gradual decrease in the difference in frequency of the yellow, unbanded and mid-banded genes in woods and other habitats from east to west across these downs. Habitat variation is greatest in the east and less to the west (p. 413). Banding genes seem to be more susceptible to those factors preventing habitat variation since both the mid- and unbanded genes stop showing habitat variation much farther east than the yellow gene.

The area effects (large areas of stable morph frequency) that have been described so far are widespread on and restricted to chalk downland. There are differences in geology, topography, flora and climate between chalk downland and other more lowland localities that have been investigated, but several area effects may occur in a single chalk region and with one exception there is no relationship between a particular area effect and any obvious environmental feature. The exception occurs on the Purbeck Hills where the border of two area effects in *C. nemoralis* coincide with a hollow in the chalk ridge about 200 ft. wide which is populated by *C. hortensis*. To the west of the hollow yellow five-bandeds are at a high frequency and to the east browns and mid-bandeds are common. As the chalk forms a narrow ridge here isolated to the north by Quaternary deposits and to the south by the sea it is possible that these area effects were derived from different founder populations.

There is no experimental evidence as to the cause of area effects but Cain & Currey (1963 *a*, *b*) argued that they are caused by selection acting at the present time. Together with Dobzhansky (1962) and Epling, Lewis & Ball (1960) who have described similar phenomena they stated that stability of morph frequencies in time and space is good evidence that these morph frequencies are maintained by selection. Cain & Currey pointed out that area effects are areas of stable morph frequency very much larger than the panmictic unit of the snails and Clarke & Murray (1962 *a*, *b*) who investigated populations of *C. nemoralis* on sand dunes found centres of stable morph frequency with steep morph ratio clines between them. They found that these clines had been stable over long periods of time relative to the generation time.

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Goodhart (1963) objected to Cain & Currey's interpretation and considered that area effects were more likely to be due to different genetic co-adaptations originating in small founder populations. Cain & Currey (1963 *c*) discussed this alternative but did not consider the evidence available supported it. Some further evidence arising from the present surveys which supports Cain & Currey's hypothesis is given below.

Several area effects occur in both *C. nemoralis* and *C. hortensis* over the same part of the western Berkshire Downs and the limits of the area effects in both species are semi-coincidental. It is true that the area effects in the two species are for different morphs but previous work (Cain & Sheppard 1954; Clarke 1960) has shown that different genetic backgrounds cause them to respond differently to visual selection and therefore it is hardly surprising that there should be some difference in their area effects as well. What is remarkable is that there should be any similarity in the limits of the area effects, and such similarity suggests that they are maintained by selection.

In *C. nemoralis* area effects are most pronounced for banding on both the western Berkshire and the Marlborough Downs and the mid-banded locus is the main one involved in these area effects. The mid-banded gene M^3 is at a high frequency in the most easterly such area effect on the Lambourn Downs but is fixed in only a few populations. The adjacent westerly area effect for banding is on the Liddington Downs where the unmodified M^- is fixed in many populations. This is also true of the next area effect to the west in district C on the Marlborough Downs (Cain & Currey 1963 *a*). In the large and most westerly area effect on the Marlborough Downs the mid-banded gene is fixed in all but a very few populations. The cline in frequency between the adjacent area effects on the Lambourn and Liddington Downs is long and gentle (approximately 5000 m). That between similar area effects on the Marlborough Downs is much shorter (over approximately 1000 m although in places much less). There are no area effects for banding on the eastern Berkshire Downs where both alleles at the mid-banded locus vary with habitat. These comparisons therefore show that there is a gradual change from variation with habitat in the east to variation with geography in the west and that there is a greater tendency to fixation of alleles at the mid-banded locus in the far west.

If these chalk downs were originally colonized by different founder populations it is difficult to understand why the effects of the resultant different co-adaptations do not show themelves either to the same degree or at least sporadically over the whole region. The rather regular changes related to an east/west axis indicate that the frequencies of the mid-banded alleles are maintained by various selective forces.

Large area effects for colour are less pronounced than those for banding, the two most clear cut being the yellow one on the Lambourn Downs and the brown one on the Marlborough Downs. The change from variation in frequency of the yellow gene mostly with habitat in the Goring district to variation more related to geography on the Lambourn Downs is regular and gradual (p. 413) and suggests the action of selection. The yellow gene is fixed in only some populations on the Lambourn Downs and the brown gene in only a few populations on the Marlborough Downs. The variation of colour morphs with habitat being restricted to valleys on both the Lambourn Downs and the Marlborough Downs (pp. 409 and 412) suggests that colour morph frequencies are much affected by local conditions. Yellow is the most common colour gene over all that part of the region

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where area effects occur except in the brown area effect in the west and other very local effects which seem to be mostly associated with valleys or slopes where pinks increase in frequency (p. 413).

The area effect for low frequency of yellows on either side of the River Thames (p. 407) is unlikely to contain two differently co-adapted genotypes separated by this barrier since it is not likely that the same genes should be at an advantage in both.

Although there is no experimental evidence at present as to an actual selective mechanism which could cause area effects Clarke (1966) in a study of clines has suggested that genotypic selection may be a cause of such effects since modifiers could produce discontinuities in a cline which need not be related to any sharp changes in the environment. He has shown how the selective effect of modifiers could under different conditions either steepen a cline or make it more shallow. Both a shallow and a relatively steep cline are found between different area effects for alleles at the mid-bandeds locus on the Berkshire and Marlborough Downs. There is some evidence that the shallow cline may have been stable for several thousand years. A sub-fossil sample dated by Professor R. J. C. Atkinson as 4000 ± 200 years old was obtained from an archaeological site in the middle of the cline. It contained recognizably distinct *C. nemoralis* and *C. hortensis* shells on which the banding pattern was quite clear. The frequency of the different banding types of *C. nemoralis* are not significantly different from those in a recent sample from nearby. This is not true of *C. hortensis* (table 14). Although this evidence for *C. nemoralis* does not rule out the selective effect of modifiers it does admit the possibility of a stable environmental selective force maintaining the cline. Goodhart (1963) agrees with Cain & Currey (1963*c*) that different co-adapted genotypes are unlikely to be equally well adapted to the same environmental conditions and therefore one area effect might be expected to expand at the expense of an adjacent one. The indication that the cline between two area effects on the Berkshire Downs has been stable for a long period therefore supports Cain & Currey's arguments that area effects are caused by selection.

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APPENDIX

TABLE 1. FREQUENCIES OF THE DIFFERENT MORPHS OF *CEPAEA NEMORALIS* IN SAMPLES TAKEN FROM THE BERKSHIRE DOWNS

Explanation of columns. Map ref.: map reference on the Ordnance Survey National Grid SU. 00000, 00300, 12345: refer to shell-banding formulae (or minor variations). fus.: shells on which two or more of the bands are fused. Spread bands: banded shells which show spreading of the band pigment across the ground colour of the shell; figures on the left of the column refer to spread five-bandeds and figures to the right of the column refer to mid-bandeds. E.U. 5 shells with more than one band but not bands 1 and 2; figures preceded by a plus sign are those that have also been included in other columns and are therefore not added to the total. Habitats: BW, beechwoods; MDW, mixed deciduous woods; HR, hedgerows; RH, rough herbage; LG, long grass; N, nettles in grass MG, mixed grasses.

	yellow						pink						brown							
map ref.	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
221799	9	—	12	—	—	8	—	—	4	—	—	2	—	—	—	—	—	—	45	RH
224797	7	—	3	17	2	10	1	—	4	7	1	1	—	—	—	—	—	—	53	RH
221801	1	—	2	9	—	—	—	—	2	2	—	—	—	—	—	—	—	—	16	RH
222807	—	3	9	14	—	—	—	—	—	3	—	—	—	—	—	—	—	—	29	RH
223795	—	—	33	11	—	—	—	—	19	—	—	—	—	—	—	—	—	—	63	DW
223796	—	—	36	4	2	—	—	—	12	4	—	—	—	—	—	—	—	—	58	RH
223796	1	—	47	28	4	—	—	—	17	—	—	1	—	—	—	—	—	—	98	RH
227789	—	21	82	12	6	1	—	4	27	1	—	—	—	—	—	—	—	—	154	RH
228796	—	—	48	51	—	3+6	—	—	17	20	1	1+1	—	—	—	—	—	—	141	LG
230786	1	—	20	14	—	3	—	1	1	10	7	—	—	—	—	—	—	—	57	DW
234783	—	—	19	5	1	—	2	—	12	2	—	—	—	—	—	—	—	—	41	RH
234786	—	—	18	1	—	2	1	—	4	—	—	—	—	—	—	—	—	—	26	RH
235788	8	1	78	11	2	—	2	—	23	3	4	—	—	—	—	—	—	—	132	BW
237773	2	—	38	12	—	—	—	—	1	1	—	—	—	—	—	—	—	—	54	LG
239827	2	—	1	—	—	—	7	—	—	6	—	1	5	—	—	—	—	—	22	RH
240826	1	—	1	—	—	—	12	—	7	—	—	—	5	—	—	—	—	—	26	LG
242774	—	—	8	—	9	—	—	—	2	2	—	—	—	—	—	—	—	—	21	RH
243821	2	1	11	17	—	—	4	2	10	31	3	—	1	—	—	—	—	2	84	LG
243801	—	—	13	5	—	—	—	—	15	2	—	—	—	—	—	—	—	—	35	LG
244798	—	—	2	—	—	—	—	—	6	—	—	—	—	—	—	—	—	—	8	RH
244799	—	—	4	—	—	—	—	—	8	2	—	—	—	—	—	—	—	—	14	RH
244829	1	—	—	10	1	—	2	—	6	15	2	—	—	—	—	—	—	1	38	RH
245822	—	1	2	5	—	—	—	2	5	11	—	—	10	—	—	—	—	—	36	RH
246790	1	—	12	2	—	—	—	—	3	—	—	—	—	—	—	—	—	—	18	BW
246828	2	—	3	—	—	1	3	—	5	15	2	—	—	—	—	—	—	—	31	RH
247769	1	—	30	6	2	—	—	—	1	1	—	—	—	—	—	—	—	—	41	RH
247790	3	—	49	3	—	—	1	—	14	2	—	—	—	—	—	—	—	—	72	DW
248797	—	—	1	—	—	—	—	—	7	3	—	—	—	—	—	—	—	—	11	RH
248828	7	—	6	9	—	+1	8	—	5	13	1	2	—	—	—	—	—	1	52	LG
249824	1	—	2	4	—	—	—	—	1	7	—	—	2	—	—	—	—	1	18	RH
249826	11	—	5	5	—	+1	11	—	4	13	—	—	—	—	—	—	—	1	50	LG

* s.b. = spread banded

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Table 1 (*cont.*)

	yellow						pink						brown							
map ref.	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
252796	4	—	13	2	—	1	6	3	15	—	—	—	—	—	—	—	—	—	44	RH
253795	4	—	16	—	—	—	9	—	14	—	—	—	—	—	—	—	—	—	43	RH
254816	—	—	33	5	—	5+1	—	—	19	6	—	2	—	—	—	—	—	—	70	LG
257793	1	—	25	3	3	—	—	—	6	1	—	—	—	—	—	—	—	—	39	BW
258819	—	—	6	3	—	—	1	—	6	—	—	—	—	—	—	—	—	—	16	RH
259791	3	—	54	6	—	—	—	—	6	2	—	—	—	—	—	—	—	—	71	BW
259812	—	—	2	—	—	—	—	—	16	—	—	—	—	—	—	—	—	—	18	LG
260810	—	—	18	—	—	—	2	—	9	2	—	1	—	—	—	—	—	—	32	LG
264789	—	—	14	—	—	—	—	—	3	1	—	—	—	—	—	—	—	—	18	N
264791	—	—	16	7	—	—	—	—	7	1	—	—	—	—	—	—	—	—	31	LG
272794	—	—	12	9	—	—	—	—	2	2	—	—	—	—	—	—	—	—	25	ST
275856	—	—	4	4	—	—	—	—	1	2	—	—	—	—	—	—	—	—	11	LG
274857	—	1	4	—	—	—	—	1	4	3	—	—	1	—	—	—	—	—	14	LG
277856	—	—	15	4	—	—	2	19	18	8	—	—	5	—	—	—	—	—	71	BW
278838	—	2	13	—	1	—	—	1	5	2	1	—	22	—	—	—	1	—	48	RH
279859	—	—	7	10	—	—	—	—	2	3	—	—	10	—	—	—	—	—	32	LG
280860	1	3	10	14	2	—	3	—	1	9	2	—	17	—	—	—	—	3	65	LG
280850	—	4	6	3	—	—	—	2	4	1	2	—	5	—	—	—	—	1	28	LG
281859	—	2	8	21	1	—	—	—	16	16	—	1	26	—	—	—	—	—	91	BW
281836	—	—	12	1	16	—	1	—	15	—	1 3	—	39	—	—	—	5	—	93	RH
282836	1	9	13	—	2 3	—	—	1	4	—	—	—	7	—	—	—	—	—	40	ST
282832	2	4	6	2	—	—	—	—	4	3	—	—	5	—	—	—	—	—	26	RH
282840	1	10	38	11	—	—	—	4	28	5	1	—	6	—	—	—	—	—	104	RH
283843	—	1	18	9	6	2	—	—	1	—	—	—	—	—	—	—	—	—	37	RH
283829	5	14	8	—	1	—	6	16	11	—	—	—	15	—	—	—	—	—	76	MG
284844	—	10	15	6	10 1	5+1	—	9	5	3	2	+2	—	—	—	—	—	—	66	BW
284862	—	—	12	4	5	—	2	1	6	10	—	—	34	—	—	—	3	11	88	RH
285822	1	21	16	3	1 2	5+1	3	4	1	—	2	2	3	—	—	—	—	—	64	LG
286857	—	—	15	5	8	—	—	—	11	5	2	—	11	—	—	—	3	—	60	LG
287815	6	5	5	—	—	1	5	1	3	—	—	—	—	—	—	—	—	—	26	RH
289858	—	—	49	11	2	3	—	—	2	—	—	—	—	—	—	—	—	—	67	RH
289845	1	6	30	1	—	2	—	11	20	—	—	2	9	—	—	—	—	—	82	N
290812	27	19	64	1	10	6	41	12	46	2	1 4	3	—	—	—	—	—	—	236	LG
291812	3	3	22	2	—	5+1	21	—	6	1	1	2	—	—	—	—	—	—	66	LG
292840	—	28	27	4	6 6	+1	—	44	38	5	1 4	+1	3	—	—	—	—	—	166	BW
293847	—	3	3	—	1	+1	11	5	7	—	3	+3	8	—	—	—	—	—	41	BW
295834	1	25	17	—	—	—	—	18	—	—	—	—	3	—	—	—	—	—	64	LG
296850	—	14	2	—	10	+2	—	7	1	—	—	—	—	—	—	—	—	—	34	LG
297849	—	17	2	—	4	+2	—	2	—	—	—	—	3	—	—	—	—	—	28	LG
297834	—	9	1	—	4	+4	—	44	3	1	—	—	—	—	—	—	—	—	62	LG

Downloaded from rstb.royalsocietypublishing.org

TABLE 1 (*cont.*)

	yellow						pink						brown							
map ref.	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
297837	1	52	4	—	11	+5	1	1	—	—	—	—	—	—	—	—	—	—	70	LG
297865	—	24	5	3	52 4	+21	1	28	3	—	11	+5	2	—	—	—	2	—	145	LG
298834	—	26	4	2	1	—	—	1	—	—	—	—	—	—	—	—	—	—	34	LG
299866	—	15	1	1	43 7	+21	—	19	2	—	2	1	3	2	—	—	—	—	96	LG
300867	—	15	5	—	30 8	1+16	1	14	4	—	—	—	2	—	—	—	1	—	81	LG
300863	—	12	—	1	8 2	+3	—	4	—	—	2	—	—	—	—	—	1	+1	30	MG
301868	—	12	1	4	12 6	+7	1	36	8	10	6 3	+4	5	—	—	—	2	—	106	LG
301830	—	27	1	1	9 1	+1	—	16	5	1	1	—	—	—	—	—	—	—	62	LG
302870	—	1	2	1	2	1	—	9	4	4	1 1	2+2	2	2	—	—	—	—	32	RH
303777	1	12	30	6	7 11	2+7	—	9	17	2	1 5	+1	—	—	—	—	—	—	103	RH
305858	—	14	3	1	20	+7	—	3	2	2	4	+2	—	—	—	—	—	—	49	MG
307804	3	4	—	1	4 1	—	—	—	—	—	—	—	1	—	—	—	—	—	14	RH
307849	2	38	5	4	29	+15	—	13	2	—	2	—	—	—	—	—	—	—	95	BW
308858	—	6	1	—	4	+2	16	5	—	—	2 1	2	—	—	—	—	—	—	37	BW
308869	—	2	3	—	5	1	—	3	4	—	—	—	3	—	—	—	1	—	22	MDW
308848	10	213	21	3	154	8+27	—	54	3	2	6	3	—	—	—	—	—	—	477	MG
308844	9	30	6	1	26	+2	—	1	—	—	—	—	—	—	—	—	—	—	73	RH*l*
309842	7	98	9	—	26 2	2+6	1	4	—	—	1	—	—	—	—	—	—	—	150	BW
311865	1	57	13	9	39 4	+5	—	12	4	—	3	—	1	—	—	—	—	—	143	BW
311864	1	14	5	5	6 1	—	—	1	—	—	1	—	—	—	—	—	—	—	34	BW
315865	—	8	6	6	5 6	1+2	—	1	2	—	—	—	—	—	—	—	—	—	35	RH
320864	—	8	1	7	—	—	—	8	6	3	—	—	—	—	—	—	—	—	33	RH
322854	—	—	—	1	—	—	—	2	1	1	—	—	—	—	—	—	—	—	5	RH
322864	—	3	3	2	—	—	—	1	1	—	—	—	—	—	—	—	—	—	10	RH
322858	—	5	8	1	—	—	—	5	10	7	—	—	—	—	—	—	—	—	36	LG
323855	—	2	9	4	—	—	—	7	7	8	—	—	—	—	—	—	—	—	37	LG
323855	—	1	7	4	—	—	—	1	12	6	—	—	—	—	—	—	—	—	31	RH
324835	10	19	3	1	5	+1	6	28	2	2	3	+2	—	—	—	—	—	—	79	BW
325851	—	22	5	—	—	—	—	3	1	—	—	—	—	—	—	—	—	—	31	RH
325833	46	119	7	5	2	+1	41	2	—	—	—	—	3	—	—	—	—	—	225	LG
325841	5	15	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	BW
325860	—	56	46	142	42 7	+6	—	31	26	89	14 2	+1	—	—	—	—	—	—	457	BW
326841	—	24	4	—	6	—	2	—	2	1	—	—	—	—	—	—	—	—	39	RH
326862	—	3	30	35	7 4	2+3	—	—	1	6	—	—	—	—	—	—	—	—	88	RH
327843	2	68	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	71	LG
331830	9	28	2	1	4	—	16	37	—	5	—	—	—	—	—	—	—	—	102	BW
332831	29	86	1	—	13	+3	18	35	1	1	2	—	—	—	—	—	—	—	186	BW
333832	32	86	6	2	7 2	+1	16	55	2	1	4	+1	—	—	—	—	—	—	213	BW
333856	2	21	14	7	1 1	1	—	—	—	—	—	—	—	—	—	—	—	—	47	BW
334857	—	32	16	—	7 4	—	—	—	—	—	—	—	—	—	—	—	—	—	59	BW

* s.b. = spread banded

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 1 (*cont.*)

	yellow						pink						brown							
map ref.	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
335858	1	50	23	3	10 6	8	—	—	—	—	—	—	—	—	—	—	—	—	101	LG
338836	15	117	27	24	13 15	+2	1	39	13	9	1	+1	—	—	—	—	—	—	274	BW
338837	17	110	27	25	21 1	+4	3	31	5	6	1	+1	—	—	—	—	—	—	247	BW
339810	17	39	4	—	15 1	+7	6	10	—	—	1	+1	—	—	—	—	—	—	93	LG
339810	25	42	1	3	18	+5	13	41	1	3	12 1	+5	—	—	—	—	—	—	160	BW
339809	10	22	—	2	11	+2	3	20	—	—	1 3	+1	—	—	—	—	—	—	72	LG
342811	4	31	—	—	9	—	1	3	—	—	2	—	—	—	—	—	—	—	50	ST
344814	15	92	—	—	32	+11	—	15	—	—	1	—	—	12	—	—	—	—	167	MG
345847	40	26	11	4	5 22	6	—	—	—	—	—	—	—	—	—	—	—	—	114	LG
345835	5	34	—	—	29	—	—	—	—	—	—	—	—	—	—	—	—	—	68	RH
348854	21	73	4	10	14 14	1+2	40	7	—	1	3 2	+1	—	—	—	—	—	—	190	LG
348829	2	6	—	1	2	+2	—	2	—	—	—	—	—	—	—	—	—	—	13	MG
349855	35	174	8	20	30 6	+4	86	4	1	—	2	—	—	—	—	—	—	—	366	LG
349814	23	45	—	—	12	+12	—	1	—	—	—	—	4	—	—	—	1	—	86	MG
351852	1	26	—	—	9	+8	—	—	—	—	—	—	—	—	—	—	—	—	36	ST
355858	2	73	—	1	10 1	+2	—	—	—	—	—	—	—	—	—	—	—	—	87	RH
354853	8	48	—	—	14	+7	—	—	—	—	—	—	—	—	—	—	—	—	70	MG
356853	12	27	—	2	50 1	+15	—	—	—	—	—	—	—	—	—	—	—	—	92	BW
358818	35	18	16	3	—	1	12	25	12	1	—	—	—	—	—	—	—	—	123	BW
358852	14	41	—	3	61	5	—	—	—	—	—	—	—	—	—	—	—	—	124	BW
358859	1	12	—	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	18	RH
359853	3	27	—	—	11	+5	—	—	—	—	—	—	—	—	—	—	—	—	41	N
359860	3	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	RH
360861	1	7	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	9	RH
361860	1	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	RH
362861	—	11	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	13	LG
364825	21	75	28	6	1	1	—	—	—	2	—	—	—	—	—	—	—	—	134	BW
365854	2	6	1	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	RH
368873	17	4	2	—	—	—	1	—	—	—	—	—	16	—	—	—	—	—	40	RH
369873	48	34	10	14	—	—	2	—	—	—	—	—	13	—	—	—	—	—	121	RH
374833	20	31	7	—	5	—	—	1	—	—	—	—	—	—	—	—	—	—	64	RH
374872	5	—	12	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—	28	RH
374844	1	38	8	35	1 4	—	—	17	5	13	5	+1	—	—	—	—	—	—	127	LG
380840	3	6	7	—	1 1	+1	1	7	8	—	2	—	3	3	—	—	—	6	48	MDW
380820	14	7	1	—	—	—	6	10	3	—	—	3	—	—	—	—	—	—	44	BW
380845	—	8	6	4	—	1	2	5	5	1	1	—	—	—	—	—	—	—	33	BW
382833	—	73	81	15	1	5	—	5	13	—	1	3	—	1	—	—	—	—	198	LG
390851	2	12	19	5	—	—	5	2	2	2	—	3	—	—	—	—	—	10	64	BW
391833	—	2	30	—	—	1	3	1	6	—	—	2	7	—	—	—	—	—	52	BW
391835	—	—	24	9	3	3	9	1	6	—	1	14	17	1	—	—	—	—	88	BW

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TABLE 1 (*cont.*)

map ref.	yellow						pink						brown						total	habitat
	00000	00300	12345	fus.	s.b.*	E.U.1	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E,U.5		
391837	—	—	43	17	5	1	5	1	32	21	6	11	16	—	—	—	—	5	163	BW
391839	—	1	32	4	3	—	6	2	18	3	3	2	7	—	—	—	—	—	81	BW
389856	3	5	7	16	4	—	1	—	1	11	—	—	14	—	—	—	—	3	65	HR
395776	—	—	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	20	LG
395768	—	—	23	8	5	—	—	—	7	1	2	—	—	—	—	—	—	—	46	RH
395850	—	25	10	1	—	—	—	—	2	—	—	—	1	4	—	—	—	—	43	BW
396850	1	11	38	4	1	—	2	2	3	—	—	—	—	1	9	—	—	—	72	RH
400848	1	1	13	3	2	1	1	1	22	2	2	—	—	—	—	—	—	—	49	BW
401822	—	8	13	8	2	—	—	—	—	—	—	—	5	—	—	—	—	—	36	RH
402792	—	—	21	9	1	—	—	—	39	26	5	—	1	—	—	—	—	—	102	BW
403875	5	1	18	14	—	—	—	—	—	—	—	—	11	—	—	—	—	11	60	HR
404844	—	3	5	—	1	—	—	1	8	3	—	1	—	—	—	—	—	—	22	HR
404873	3	—	33	8	—	—	—	—	—	—	—	—	19	—	—	—	—	—	63	HR
407870	—	—	40	3	1	2	—	—	—	—	—	—	10	—	—	—	—	—	56	N
407865	9	—	14	8	7	—	—	—	4	—	1	—	1	—	—	—	—	—	44	RH
408864	16	—	19	18	6	1	7	—	3	8	3	—	—	—	—	—	—	—	81	RH
408868	1	—	30	19	—	8	—	—	1	—	—	—	14	—	—	—	—	—	73	RH
408817	—	—	16	4	—	—	17	—	67	8	1	—	—	—	—	—	—	—	113	BW
410858	2	—	19	11	—	—	1	—	20	7	1	—	—	—	—	—	—	—	61	RH
424886	14	1	10	2	—	—	12	2	18	11	—	—	4	—	—	—	—	5	79	BW
435845	12	—	43	—	1	—	—	—	12	4	—	—	—	—	—	—	—	—	72	ST
439889	41	—	2	10	1	—	16	—	7	8	—	1	—	—	—	—	—	—	87	RH
439841	—	—	4	—	—	—	17	1	1	—	1	—	—	—	—	—	—	—	24	BW
444836	—	—	20	6	1	—	—	—	15	4	—	—	—	—	—	—	—	—	46	ST
445855	—	—	9	1	—	—	—	—	3	—	—	—	20	—	—	—	—	—	33	BW
446875	12	1	2	4	—	—	3	6	4	13	—	—	2	—	1	—	—	1	49	RH
447877	6	2	3	2	1	—	11	7	—	—	—	—	2	—	—	—	—	—	34	LG
448858	3	1	8	7	—	+1	—	—	—	—	—	—	4	—	—	—	—	—	23	MDW
455832	—	2	57	—	1	—	6	3	12	—	—	—	—	—	—	—	—	—	81	LG
457851	—	1	1	3	—	—	100	—	3	8	—	—	—	—	—	—	—	—	116	RH
459854	17	2	2	—	—	—	8	3	1	—	—	—	6	—	—	—	—	—	39	LG
459869	—	—	9	—	—	—	—	—	6	1	—	—	19	—	4	—	—	—	39	MDW
459829	1	—	11	2	—	—	—	—	5	1	1	—	—	—	—	—	—	—	21	HR
460875	8	—	25	7	—	1	—	—	5	2	1	—	15	—	—	—	—	—	64	LG
461878	2	—	9	1	—	—	—	—	2	1	—	—	1	—	—	1	—	—	17	RH
467831	7	12	—	—	—	—	4	13	4	—	—	—	22	—	—	—	—	—	62	RH
468833	—	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	LG
475825	—	11	12	5	—	—	17	8	5	—	—	1	13	—	—	—	—	15	87	MDW
476908	4	5	15	3	—	—	2	1	—	—	—	5	—	—	—	—	—	—	35	N
479825	1	—	2	—	—	—	1	—	1	2	—	1	—	—	—	—	—	—	8	RH

* s.b. = spread banded

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TABLE 1 (*cont.*)

	yellow						pink						brown							
map ref.	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
480827	1	—	19	—	—	1	8	—	4	2	—	2	—	—	—	—	—	—	37	LG
482821	—	3	—	1	—	7	—	11	8	1	—	14	—	—	—	—	—	—	45	RH
482821	1	13	17	—	—	17	—	24	12	2	—	20	—	—	—	—	—	—	106	LG
483875	7	1	6	3	—	—	3	3	11	2	—	—	—	—	—	—	—	—	36	N
483875	—	4	16	47	—	7	—	16	26	39	—	2	—	—	—	—	—	—	157	RH
485846	—	—	9	—	3	—	2	—	25	6	6	—	20	—	—	—	—	34	105	
490836	7	—	14	—	—	—	—	—	8	1	—	—	2	—	—	—	—	—	32	HR
490812	—	—	2	—	1	—	—	—	2	2	2	—	—	1	—	—	—	—	10	RH
493823	4	—	24	25	—	11+4	1	—	22	31	—	6	—	—	—	—	—	—	124	LG
495812	—	7	18	3	—	3	—	6	13	5	—	1	6	—	—	—	—	—	62	RH
497885	—	—	3	—	1	—	—	15	17	4	2	—	23	—	1	—	—	—	66	RH
508804	—	4	1	1	—	—	—	8	7	1	—	—	5	—	—	—	—	5	32	MD
517802	—	2	—	—	—	—	—	6	—	—	—	—	2	—	—	—	—	—	10	BW
527807	—	2	6	1	—	1	2	1	15	1	1	5	1	1	—	—	—	—	37	HR
530814	—	2	6	—	—	—	2	27	29	2	6	13	—	—	—	—	—	—	87	BW
530814	—	2	6	—	—	—	3	17	17	7	3	8	—	—	—	—	—	—	63	BW
534796	—	3	8	3	—	—	—	—	4	2	—	—	1	—	—	—	—	—	21	RH
544832	16	—	24	9	—	—	5	—	4	2	—	7	1	—	—	—	—	—	68	LG
544823	—	1	17	1	—	—	1	—	15	1	—	—	5	—	—	—	—	—	41	LG
545810	—	—	2	—	—	—	—	3	6	1	1	—	3	1	—	—	—	—	17	HR
549841	8	—	6	1	—	1	5	1	8	2	2	1	2	—	—	—	—	—	37	LG
550851	4	—	5	2	—	—	6	—	21	15	13	6	23	—	—	—	—	—	95	LG
550851	3	—	1	5	1	—	12	—	7	28	4	6	23	—	—	—	—	1	91	LG
553845	3	—	18	3	—	—	17	—	6	2	2	5	—	—	—	—	—	—	56	LG
554846	9	—	11	11	—	7	22	—	15	11	1	1	—	—	—	—	—	—	88	LG
554809	—	—	20	7	—	—	—	1	14	5	—	—	—	—	—	—	—	—	47	LG
556837	1	2	5	4	—	—	28	9	12	5	—	—	—	—	—	—	—	—	66	BW
559812	1	4	6	—	1	1	17	13	10	7	1	—	3	—	—	—	—	—	64	LG
561807	—	—	72	20	4	2	—	—	43	12	—	—	—	—	—	—	—	—	153	LG
562812	7	1	15	2	2	—	18	1	24	13	—	1	1	—	—	—	—	—	85	RH
563812	—	7	4	4	—	—	2	7	12	13	—	—	—	—	—	—	—	—	49	LG
564813	—	3	15	3	—	—	7	13	18	9	1 1	—	—	—	—	—	—	—	70	LG
565853	—	—	80	14	—	1	—	1	18	11	—	—	1	—	—	—	—	—	126	RH
566837	—	—	53	9	2	—	6	2	71	7	1	1	8	—	—	—	—	—	160	LG
566822	—	2	2	—	—	—	20	31	13	3	—	1	44	—	—	—	—	—	116	BW
566837	—	—	39	5	—	1	1	—	32	7	—	1	1	—	—	—	—	—	88	LG
566816	—	1	8	1	—	—	3	2	8	1	1	—	—	—	—	—	—	—	25	ST
567817	1	4	5	1	1	—	31	30	5	7	1 3	14	17	—	—	—	—	—	120	BW
568822	—	—	—	—	—	—	8	10	4	—	—	—	3	—	—	—	—	—	25	BW
571837	—	4	10	1	—	1	—	4	18	13	—	1	—	—	—	—	—	—	52	MDW

Downloaded from rstb.royalsocietypublishing.org

TABLE 1 (*cont.*)

	yellow						pink						brown							
	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
573802	—	12	11	—	2	—	3	7	5	1	—	—	8	—	—	—	—	—	49	LG
575825	—	1	9	1	—	2	—	—	3	4	—	1	—	—	—	—	—	—	21	LG
581801	—	—	3	2	1	—	12	—	32	3	3	4	4	—	—	—	—	—	64	LG
582808	—	1	3	—	—	—	13	2	14	—	—	—	—	—	—	—	—	—	33	LG
584848	—	—	7	—	—	—	—	—	—	—	—	1	10	—	—	—	—	—	18	HR
586801	2	1	2	—	—	—	30	7	2	7	—	1	4	—	—	—	—	—	56	BW
587849	—	—	12	—	—	—	7	—	—	—	—	—	8	—	—	—	—	—	27	HR
587806	1	3	9	1	—	1	10	12	12	5	—	3	5	1	—	—	—	4	67	LG
587805	6	8	10	4	—	2	25	27	10	16	3	—	21	—	1	—	—	1	134	LG
588804	4	5	1	—	—	—	30	29	4	2	—	—	7	—	—	—	—	—	82	BW
588850	—	—	15	3	—	—	1	—	—	—	—	—	18	—	—	—	—	1	38	HR
588806	—	1	1	—	—	—	32	10	—	3	—	—	6	1	1	—	—	—	55	BW
588804	—	1	—	—	—	—	48	12	8	5	—	—	—	—	—	—	—	—	74	BW
589801	1	—	6	—	—	—	1	—	—	—	—	1	1	—	—	—	—	—	10	RH
589811	—	5	22	5	1	1	3	8	27	10	—	1	12	—	—	—	—	—	95	LG
589807	—	4	2	—	—	—	16	9	15	12	—	—	22	3	4	1	—	5	93	LG
589806	2	2	5	—	—	—	12	10	4	1	—	1	6	—	—	—	—	2	45	LG
589806	—	4	2	—	—	—	15	18	8	—	—	—	4	1	3	—	—	6	61	LG
592803	1	3	1	—	—	—	15	7	5	—	—	—	1	—	—	—	—	—	33	BW
615815	1	3	4	3	—	—	—	—	3	2	—	—	1	—	—	—	—	—	17	RH
617815	1	2	1	1	—	—	11	8	3	4	—	5+1	6	—	—	—	—	—	42	LG
616795	2	—	1	2	—	—	19	1	1	4	—	—	6	—	—	—	—	—	36	LG
617815	3	3	1	2	1	—	26	22	8	4	4	7	29	—	—	—	—	—	110	LG
619792	—	—	2	—	—	—	10	2	3	2	1	2	—	—	—	—	—	—	22	MDW
619792	—	—	1	—	—	—	9	1	—	1	—	—	6	—	—	—	—	—	18	MDW
625849	—	4	4	6	—	—	—	12	—	3	—	—	—	—	2	3	—	—	34	HR
625849	—	9	12	—	—	—	—	—	5	2	—	—	27	—	—	—	—	—	55	RH
627851	—	23	8	4	—	—	—	6	2	—	—	—	3	—	—	—	—	—	46	RH
626849	—	11	9	5	—	—	—	6	4	2	—	—	23	—	—	—	—	—	60	RH
645777	—	2	4	8	1	2	2	—	9	12	2	2	19	—	—	3	—	1	67	LG

* s.b. = spread banded

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Table 2. Frequencies of the different morphs of *Cepaea hortensis* taken from the Berkshire Downs

Explanation of columns. Map ref: map reference on the Ordnance Survey National Grid SU.00000: unbanded shells. Hz.: shells with hyalozonate bands. Hz. fus.: shells with hyalozonate fused bands. Pale: shells with pale pigmented bands. Pale fus.: shells with pale fused bands. Normal: shells with dark pigmented bands. E.U.5: shells with more than one band but not 1 or 2. Habitats BW: beechwoods; MDW: mixed deciduous woods; HR: hedgerows; RH: rough herbage; LG: long grass, N: nettle patches in grass. The brown shells for those samples that contain them are, for convenience, shown at the end of the table.

	yellow									
map ref.	00000	hz.	hz. fus.	pale	pale fus.	normal	normal fus.	E.U.5	total	habitat
199795	20	—	—	—	—	28	4	—	54	RH
204798	15	—	—	4	—	24	5	—	48	RH
205799	12	2	—	13	—	17	1	1	46	RH
208802	2	8	—	17	—	14	2	—	43	RH
211803	8	3	—	—	—	43	3	—	57	RH
212804	—	7	1	17	2	12	6	—	45	RH
216806	6	16	—	56	—	20	4	13pb	115	RH
219806	24	5	2	13	—	11	2	—	57	RH
217806	—	10	1	12	—	3	—	—	26	RH
219804	35	20	4	21	—	12	4	5	101	LG
221801	44	6	1	24	1	15	1	1pb	93	RH
222807	16	9	1	47	1	72	2	1pb	149	RH
223796	4	24	6	40	9	23	16	—	122	RHT
223796	4	28	10	39	16	14	7	—	118	RHT
224799	12	14	4	16	5	4	3	1pb	61	LG
223795	13	47	7	54	14	33	7	—	175	RHT
225807	1	1	—	5	—	31	2	1pb	41	RH
226809	2	20	—	9	—	6	—	—	38	RH
229812	8	3	—	11	—	12	2	2pb	38	RH
232812	—	13	7	17	17	8	4	3pb	68	RHT
234815	—	5	—	6	—	1	2	1pb	15	RH
234783	15	—	—	4	1	—	1	—	21	RH
235830	1	1	—	—	1	24	1	2	30	HR
235821	—	8	1	10	1	7	—	8pb	35	RH
238805	5	9	—	—	—	24	12	—	50	RHN
239827	—	21	3	10	2	1	6	—	43	RH
239779	81	—	—	—	—	4	—	—	85	RH
240835	8	—	—	—	—	30	3	—	41	N
240826	—	11	—	15	—	3	1	1	31	LG
242774	35	—	—	2	2	20	12	—	77	RH
242801	29	—	—	—	—	31	25	—	85	RH
243821	—	1	—	—	—	12	2	—	15	LG
244829	—	—	—	—	—	6	13	—	19	RH
244798	27	—	—	3	—	36	32	—	98	RH
244799	22	—	—	—	—	30	25	—	77	RH
245822	10	—	—	5	—	7	6	—	28	RH
246828	24	—	—	—	—	25	29	—	78	RH
247835	4	14	15	12	5	2	2	—	54	RH
248797	—	3	—	8	2	1	1	1	16	LG
248795	3	13	—	30	—	15	13	—	74	RH
248828	4	—	—	—	—	—	3	—	7	LG
248833	17	6	10	—	—	20	21	1	75	RH
249829	33	9	3	—	—	12	—	—	57	RH
249824	53	1	—	3	1	9	2	—	69	RH
250838	2	7	3	11	—	5	—	—	28	RH
252828	4	23	4	15	—	9	3	—	58	RH
252839	3	3	3	9	4	11	5	3	41	RH
253764	—	28	—	19	—	2	—	—	50	RH
254827	48	3	—	3	—	—	—	—	54	RH
254824	5	110	6	34	2	32	14	1pb	203	RH
256822	12	1	—	4	—	18	11	1pb	47	RH

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TABLE 2 (*cont.*)

	yellow									
map ref.	00000	hz.	hz. fus.	pale	pale fus.	normal	normal fus.	E.U.5	total	habitat
258819	8	53	3	37	5	14	5	—	127	RH
259844	—	25	—	5	5	—	—	—	35	RH
259756	—	27	1	6	2	—	—	1pb	37	RH
259816	31	1	—	—	—	35	14	—	81	RH
260845	4	1	2	23	10	13	11	—	65	RH
261792	27	24	20	7	—	2	2	—	100	N
262547	6	1	7	3	8	3	2	—	41	RH
264791	—	5	—	2	—	—	—	—	7	LG
264789	—	27	—	26	—	—	—	1pb	54	N
265833	—	14	2	35	4	—	—	4pb	59	RH
267831	—	6	4	—	2	26	9	—	47	RH
265837	23	67	—	—	—	17	—	3	110	RH
268838	3	60	—	23	1	63	5	1	156	RH
268848	7	—	—	—	—	—	7	—	14	LG
268854	33	—	—	4	3	3	3	1	47	LG
269827	—	5	—	—	—	42	13	—	60	RH
269847	21	—	—	15	—	15	6	2pb	59	RH
270841	—	39	3	27	—	2	—	3pb	74	RH
271825	—	8	11	24	8	29	16	—	96	RH
271856	41	—	—	—	—	1	5	—	47	RHN
273770	4	5	1	12	—	5	3	—	30	HR
273843	7	27	—	25	—	19	2	—	80	RH
273859	62	—	—	—	—	14	14	—	91	LG
294857	—	—	—	—	—	14	20	—	34	LG
274843	9	10	1	33	4	2	—	10pb	69	RH
275856	6	—	—	—	—	62	20	—	88	LG
276840	25	24	4	71	4	12	1	31	172	RH
283854	38	—	—	1	—	15	—	—	54	LG
283868	13	—	—	—	—	9	—	—	22	RH
284859	25	—	—	—	—	1	—	—	26	RH
284865	44	—	—	—	—	3	7	—	54	RHN
284868	24	—	—	2	—	5	—	—	31	RH
284870	56	—	—	—	—	60	10	—	126	LG
286854	8	1	—	—	—	1	1	—	11	LG
286856	33	—	—	4	—	27	11	—	75	RH
286857	56	—	—	—	—	40	13	—	109	LG
287883	3	—	—	—	—	43	35	—	81	RH
289858	9	1	—	—	—	65	1	1	77	RH
289872	19	—	—	18	3	20	10	—	70	LG
293847	23	—	—	—	—	3	8	—	34	BW
293872	20	2	—	21	19	9	18	1pb	90	RH
296850	2	—	—	—	—	17	10	—	29	LG
297849	3	—	—	3	—	28	10	—	44	LG
297865	—	—	—	13	2	24	4	—	43	ST
297871	8	—	—	5	—	9	1	1pb	24	RH
299866	—	—	—	7	5	21	14	—	47	ST
299873	1	2	—	12	10	52	27	—	104	RH
300777	1	2	—	—	—	45	—	—	48	RH
300867	—	—	—	—	—	6	—	—	6	LG
301868	18	—	—	—	—	2	—	—	20	LG
301801	3	6	—	26	1	8	7	7pb	59	RH
302870	12	—	—	—	—	9	5	1	27	RH
303874	12	—	—	7	—	28	—	—	49	N
303777	51	3	—	4	—	30	12	—	134	RH
305872	13	3	—	1	—	13	12	—	42	RH
307779	—	2	—	2	—	57	25	—	117	RH
307804	13	9	1	4	—	13	9	—	64	RH
308869	2	5	—	—	—	6	2	—	15	MDW
311865	3	—	—	2	1	6	8	—	20	BW

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TABLE 2 (*cont.*)

	yellow									
map ref.	00000	hz.	hz. fus.	pale	pale fus.	normal	normal fus.	E.U.5	total	habitat
311874	1	—	—	—	—	16	1	2	20	RH
313873	1	4	—	1	2	22	4	—	34	LG
313872	1	6	4	9	—	8	6	—	40	RH
315865	13	—	—	—	—	21	—	—	34	RH
319863	29	—	—	—	—	12	4	—	45	RH
321785	4	—	2	3	—	12	16	—	51	RH
322854	—	—	—	—	—	9	13	—	22	RH
322872	1	1	—	6	2	24	—	—	34	RH
324942	17	—	—	—	—	4	5	—	26	LG
326862	3	—	—	9	4	46	66	—	128	RH
327843	—	5	—	—	—	—	—	—	5	LG
327847	22	16	11	—	5	32	18	—	107	RH
329859	—	14	2	6	1	—	—	—	23	RH
330859	—	33	7	—	—	18	8	—	66	RH
332862	3	49	2	14	1	—	2	—	71	RH
335858	14	—	—	—	—	—	6	—	20	LG
336873	1	5	6	5	3	4	7	—	31	RH
336867	3	18	5	3	—	11	1	—	41	HR
337872	1	10	16	2	1	1	—	—	31	N
338571	2	10	7	11	4	0	1	—	35	RHN
339810	1	—	—	—	1	17	8	2	36	BW
339867	7	4	—	—	—	18	8	—	37	HR
341871	1	13	4	1	—	24	18	—	61	HR
343854	—	17	4	—	—	2	3	—	26	RH
347811	—	1	—	23	—	31	11	1	74	RH
349871	7	1	—	—	—	9	4	—	22	RH
354871	6	—	—	—	—	58	20	—	84	RH
355858	23	—	183	16	—	54	40	—	317	RH
357869	17	—	—	—	—	27	8	—	52	RH
358859	33	6	6	8	12	41	55	—	162	RH
359860	9	9	3	4	—	8	5	—	38	RH
359861	2	3	5	7	2	—	18	—	37	RH
359870	54	—	—	—	—	6	23	—	88	RH
360861	10	40	32	1	3	32	41	—	159	
361869	14	1	—	—	—	11	3	—	32	LG
360868	2	1	—	—	—	12	7	—	23	LG
361860	4	17	10	—	—	16	13	—	60	RH
362861	—	11	6	—	—	12	7	—	36	LG
364859	3	—	—	—	—	17	3	—	44	RH
364870	37	4	—	—	2	16	26	—	102	RH
365854	7	8	—	5	—	18	7	—	45	RH
367873	15	13	10	20	1	5	6	4hz +	80	RH
367756	—	—	—	10	—	7	6	—	23	RH
368873	17	1	—	2	—	—	1	—	21	RH
374844	2	—	—	—	—	4	6	—	12	LG
381776	4	—	—	15	—	14	32	—	70	MDW
386753	14	—	—	4	—	13	4	4	45	RH
395776	—	—	—	—	—	28	1	—	29	LG
399780	1	—	4	—	17	10	—	—	33	RH
414853	—	2	—	—	23	—	—	3	28	RH
415845	—	7	—	4	—	11	1	7pb	30	RH
415850	—	1	1	11	4	10	9	12pb	48	RH
416847	—	—	—	16	—	—	—	20pb	36	RH
441825	—	—	—	—	—	12	2	2	16	RH
454829	1	—	—	—	—	19	8	—	28	HR
459829	7	1	—	1	—	17	11	7	44	HR
467831	26	—	—	—	—	18	7	8pb	59	LG
474830	—	—	—	—	—	16	7	2	25	RH
479825	—	4	2	22	13	11	8	—	63	RH

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TABLE 2 (*cont.*)

	yellow									
map ref.	00000	hz.	hz. fus.	pale	pale fus.	normal	normal fus.	E.U.5	total	habitat
482812	—	1	2	7	—	20	6	—	36	RH
490812	1	—	—	8	—	24	16	1	50	MDW
504877	1	—	—	—	—	28	—	18pb	47	N
505874	10	—	—	12	—	11	10	2	45	RH
511805	1	—	—	—	—	7	8	—	16	MDW
547807	—	—	—	—	—	11	8	—	19	MDW
556837	10	—	—	—	—	14	11	—	57	BW
566822	5	—	—	—	—	2	—	—	7	BW
567817	3	—	—	—	—	2	11	2pb	18	BW
581801	—	—	—	1	—	1	2	—	4	LG
592803	—	—	—	1	—	1	2	—	4	MDW
625849	7	—	—	—	—	—	—	—	7	HR
657888	3	—	—	—	—	13	9	—	25	HR
483823	—	—	—	—	—	26	4	—	30	LG

	brown		
map ref.	00000	12345	fus.
199795	—	2	—
224799	2	—	—
226809	1	—	—
242774	2	1	3
253764	—	—	1
258819	—	1	1
260845	1	—	—
261792	2	4	12
262847	11	—	—
301801	1	—	—
303874	—	2	—
303777	7	3	24
307779	1	13	17
307804	5	6	4
313782	1	—	5
321785	5	—	9

	brown		
map ref.	00000	12345	fus.
327847	—	1	2
339810	4	1	2
347811	—	1	6
349871	—	—	1
355858	—	—	1
359870	2	2	1
361869	—	—	3
360868	—	—	1
364859	21	—	—
367870	7	3	7
367873	6	—	—
381776	5	—	—
386753	4	2	—
339780	—	—	1
479825	—	1	2
556837	2	4	16

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Table 3. Composition of random samples of *Cepaea nemoralis* from the Purbeck Hills

	yellows						pinks						browns							
map ref.	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
013813	1	1	3	—	—	—	—	10	31	2	—	—	4	—	—	—	—	—	52	ST
949824	2	3	5	1	—	—	—	5	11	2	—	—	1	—	—	—	—	—	30	LG
944825	—	9	3	—	1	—	2	26	4	3	—	—	7	—	—	—	—	—	55	MDW
923817	2	10	1	—	—	1	—	3	—	—	—	1	10	1	—	—	—	—	29	ST
910816	26	21	1	1	—	—	1	4	—	—	—	—	19	—	—	—	—	—	73	ST
909819	4	—	—	—	—	—	1	2	—	2	1	—	10	6	2	1	—	—	29	MDW
909819	4	—	—	—	—	—	2	4	—	4	—	—	10	3	2	—	1	—	30	MDW
909818	1	—	—	—	—	—	1	1	1	—	—	—	5	3	—	—	—	—	12	MDW
909815	8	6	1	—	—	—	1	—	—	—	—	—	13	—	—	—	—	—	30	ST
909818	2	—	1	—	—	—	3	—	—	—	—	—	2	2	1	1	—	—	12	MDW
868805	—	5	4	—	—	—	—	—	—	—	—	—	2	6	2	3	—	—	22	RH
867808	—	5	8	1	—	—	1	2	—	—	—	—	2	9	3	2	—	1	34	ST
866807	3	7	7	—	—	1	—	3	1	—	—	—	—	11	9	—	1	—	43	ST
864807	2	12	4	—	1	1	—	4	—	—	—	3	1	11	6	—	—	—	45	ST
860806	2	12	5	—	—	1	—	1	2	—	—	—	—	22	5	—	1	2	53	ST
849806	—	1	6	12	1	—	—	—	—	—	—	—	—	—	—	—	—	—	20	MDW
846803	—	9	26	20	19	3	—	—	—	1	—	—	1	—	—	—	—	—	79	ST
845804	—	6	29	3	12	—	—	2	3	—	—	—	—	—	—	—	—	—	55	ST
845803	—	19	58	3	2	6	—	—	—	—	—	—	—	—	—	—	—	1	89	ST
842802	1	7	40	5	—	5	—	—	5	—	—	1	—	—	—	—	—	—	64	ST
842804	—	12	56	—	—	—	—	1	11	—	—	—	—	—	—	—	—	—	80	ST
836804	1	3	13	1	—	5	2	6	18	1	—	5	—	—	2	—	—	1	58	ST
836803	—	10	13	13	12	—	—	—	—	1	4	—	2	—	—	—	—	—	55	ST
834804	1	6	27	4	3	1+1	—	6	13	1	—	—	—	1	1	—	—	1	65	ST
834802	2	9	23	8	11	2	1	4	4	—	—	—	1	—	—	—	—	—	65	ST
833802	4	40	20	8	18	1	—	3	1	—	—	—	—	—	—	—	—	—	95	LG
832804	1	8	17	5	18	1	—	—	4	—	3	—	1	—	—	—	—	—	58	ST
829802	—	2	7	8	18	1	—	—	—	—	—	—	1	—	—	—	—	1	38	ST
828804	—	2	9	2	14	1	—	—	1	1	5	—	4	—	—	—	—	—	39	ST
826802	6	5	23	5	14	—	—	1	1	—	2	—	10	—	—	—	—	—	67	ST
825804	1	2	16	9	10	—	—	—	1	—	1	—	2	—	—	—	—	—	42	ST
795806	—	1	2	1	—	—	—	1	1	—	1	—	—	—	—	—	—	—	7	LG
795807	—	3	7	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	LG

* s.b. = spread banded

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 4. Composition of random samples of *Cepaea hortensis* from the Purbeck Hills

	yellows					pinks						
map ref.*	00000	12345	fus.	E.U.5	spread banded	00000	12345	fus,	E.U.5	spread banded	total	habitat
022810	3	5	5	—	—	—	2	—	1	—	16	LG
019810	3	16	6	—	—	—	8	—	—	—	33	ST
982817	1	17	10	—	—	1	3	—	—	—	32	ST
976820	2	21	1	—	—	—	—	1	—	—	25	ST
974817	4	10	—	1	—	1	8	—	2	—	26	HR
970819	8	29	5	2	—	4	6	1	—	—	55	HR
964821	14	32	5	1	—	4	7	—	—	—	63	HR
958823	18	20	2	—	—	8	2	1	—	1	52	MDW
944825	6	8	2	—	—	4	5	—	4	—	29	MDW
943823	—	17	1	—	—	—	—	1	—	—	19	RH
936817	3	23	—	1	—	2	3	—	—	—	32	HR
934824	—	11	6	—	—	—	3	2	—	—	22	MDW
929821	—	22	—	2	—	—	—	—	—	—	24	LG
927819	1	12	1	2	—	—	3	—	—	—	19	HR
917817	2	3	—	—	—	—	5	—	—	—	10	MDW
916806	3	11	2	—	—	—	2	—	—	—	18	HR
914812	10	7	—	—	—	3	6	—	—	—	26	MDW
911818	4	6	2	—	—	2	9	3	—	—	26	HR
909818	—	9	3	—	—	5	9	3	—	—	29	MDW
909819	10	25	26	—	2	24	26	27	—	8	148	MDW
906816	2	25	2	11	—	—	5	—	—	—	45	HR
906812	5	22	3	—	—	1	6	—	—	—	37	RH
905815	14	5	—	—	—	—	7	4	—	—	30	ST
855805	6	13	—	—	—	—	2	—	—	—	21	ST
852803	2	17	—	—	—	—	4	—	—	—	23	ST
851802	1	10	4	—	—	1	7	3	—	—	26	ST
850805	2	21	—	—	1	—	9	—	—	—	33	HR
849806	8	26	10	—	5	8	25	6	—	3	91	MDW
849802	2	7	1	—	—	—	5	1	—	—	16	ST
825804	12	2	1	—	—	—	—	—	—	—	15	ST
820810	3	5	5	3	—	—	3	1	1	—	21	LG
818804	—	3	—	—	—	—	1	—	—	—	4	ST
815810	15	8	—	—	—	—	—	—	—	—	23	RH
813820	1	22	—	—	—	—	—	—	—	—	23	LG
810814	3	29	2	2	—	1	4	—	—	—	41	RH
809837	1	27	21	5	—	—	1	—	—	—	55	ST
802840	8	18	—	—	—	—	8	—	—	—	34	LG
801813	10	30	2	—	—	4	3	—	—	—	39	RH
796834	4	22	1	1	—	1	2	—	—	—	31	RH
795810	—	43	12	—	—	—	4	—	—	—	59	ST
795807	—	8	1	—	—	—	2	—	—	—	11	LG
789809	1	75	—	—	—	5	—	—	—	—	81	ST
776845	1	18	2	4	—	—	—	—	—	—	25	LG
767849	9	20	2	—	—	6	12	2	—	—	54	RHN
766845	1	30	4	3	—	—	1	—	—	—	40	RH
766839	—	19	—	2	—	—	—	—	—	—	21	RH
762821	2	34	1	—	—	—	—	—	—	—	37	HR
761850	25	3	2	—	—	17	6	4	—	—	57	BW
754825	6	21	—	—	—	—	—	—	—	—	27	LG
748851	6	14	—	—	—	—	2	1	—	—	23	LG
745827	—	21	—	—	—	—	—	—	—	—	21	RH
744844	5	15	1	—	—	5	9	6	—	—	42	MDW
743840	16	23	1	—	—	4	5	—	—	—	58	RHN
735823	22	30	6	2	—	—	—	—	—	—	63	RH
731829	2	14	3	—	—	1	1	—	—	—	22	HR
715830	8	15	6	—	—	1	4	1	—	—	35	LG
709830	17	28	2	—	1	—	2	1	—	—	51	RH

The following samples contain brown shells: 767849, two brown unbanded and one brown 12345; 766845, one brown (12345) 744844, one brown unbanded; 743840, two brown unbandeds, four brown 12345, two brown banded with fusions; 735823, two brown 12345, one brown banded with fusions; 731829, one brown 12345. * Ordinance Survey National Grid ST.

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TABLE 5. COMPOSITION OF RANDOM SAMPLES OF *CEPAEA NEMORALIS* FROM SOMERSET

	yellows						pinks						browns							
map ref.†	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	00000	00300	12345	fus.	s.b.*	E.U.5	total	habitat
709369	—	—	—	—	—	—	4	5	—	—	1	—	1	1	—	—	—	—	12	MDW
699357	—	—	—	1	—	—	2	—	—	1	—	—	—	—	—	—	—	—	4	MDW
697285	—	—	—	—	—	—	—	2	2	—	—	—	9	1	—	—	—	—	14	Copse/HR
694282	4	—	—	—	—	—	3	6	5	4	2	—	7	—	—	—	—	—	31	MDW
682289	—	—	—	—	—	—	7	—	2	—	—	—	1	—	—	—	—	—	10	BW
678309	—	—	1	—	—	—	—	—	2	—	—	—	8	—	—	—	—	—	11	HR
669361	—	2	2	—	—	—	1	1	10	—	—	—	5	—	—	—	—	—	21	MDW
667375	—	2	—	—	—	—	8	2	1	—	—	1	—	—	—	—	1	—	15	MDW
663288	—	1	—	2	—	—	29	4	2	1	—	—	6	—	—	—	—	1	46	BW
662300	—	—	1	—	—	—	11	—	6	—	—	—	10	2	6	—	—	1	37	MDW

* s.b. = spread banded. † Ordinance Survey National Grid ST.

TABLE 6. PART I. COMPOSITION OF RANDOM SAMPLES OF *CEPAEA HORTENSIS* TAKEN FROM SOMERSET BY CARTER

	yellow					pink					brown						
map ref.*	00000	12345	fus.	E.U.5	others	00000	12345	fus.	E.U.5	others	00000	12345	fus.	E.U.5	others	total	habitat
648314	8	15	4	—	—	9	2	1	—	—	—	—	—	—	—	39	HR
648314	1	21	11	—	—	2	1	—	—	—	—	—	—	—	—	36	H
659309	—	24	8	—	1sp	2	2	—	—	—	2	—	—	—	—	39	RH
659309	3	43	4	3	—	4	3	—	—	—	—	—	—	—	—	60	RH
662300	20	11	5	—	—	—	—	—	—	—	—	—	—	—	—	36	MDW
662312	13	16	1	—	—	—	—	—	—	—	17	7	3	—	—	57	MDW
663288	2	12	—	1hz.	—	—	—	—	—	—	—	—	—	—	—	15	BW
669361	26	19	5	—	—	—	—	—	—	—	—	—	—	—	—	50	MDW
675311	1	17	5	—	—	2	2	1	—	—	—	3	1	—	—	32	HR
678309	8	11	4	—	—	1	1	1	—	—	—	1	—	—	—	27	HR
682289	7	13	1	—	—	—	6	1	—	—	—	—	—	—	—	28	BW
683288	4	14	—	—	—	—	3	—	—	—	—	—	—	—	—	21	HR
683288	4	24	3	—	—	—	7	—	—	—	—	—	—	—	—	38	HR
684352	2	11	15	—	—	—	—	3	—	—	6	—	—	—	—	37	HR
694282	8	14	2	—	—	—	2	—	—	—	3	—	—	—	—	29	MDW
697285	1	6	—	—	—	3	2	—	—	—	—	—	—	—	—	12	HR
697285	1	11	3	—	—	6	1	—	—	—	—	—	—	—	—	22	N
699357	1	31	4	1	—	1	17	3	6	—	—	4	—	—	—	68	MDW
709369	13	20	2	3	1sp	3	8	—	—	—	—	—	—	—	—	50	MDW

* Ordinance Survey National Grid ST

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Table 6. Part II. Composition of random samples of *Cepaea hortensis* taken from Somerset by C. Diver

map ref.*	yellow				pink				brown				total	habitat
	00000	12345	E.U.5	others	00000	12345	E.U.5	others	00000	12345	E.U.5	others		
647324	3	53	—	—	—	1	—	—	1	—	—	—	58	HR
648322	2	38	200300	—	—	3	—	—	—	—	—	—	45	RH
648319	4	12	—	—	—	—	—	—	—	—	—	—	16	RH
647314	—	29	—	—	4	7	—	—	—	—	—	—	40	RH
648314	10	20	1	—	1	5	—	—	1	—	—	—	38	RH
675311	24	92	3hz	—	4	—	—	—	—	24	—	—	147	HR
675311	10	45	—	—	3	—	—	—	1	3	—	—	62	HR
678309	8	15	—	—	—	—	—	—	6	—	—	—	29	RH
659309	6	126	—	—	5	9	—	—	13	—	—	—	159	RH
683288	50	67	3hz	—	13	26	—	—	2	—	—	—	161	HR
683288	11	24	4hz	—	5	7	—	—	1	—	—	—	52	HR
690284	8	65	1hz	—	2	121	—	—	38	2	—	—	237	RH
690285	4	34	—	—	3	45	—	—	13	1	—	—	100	RH
295285	2	13	1	—	—	1	—	—	—	—	—	—	17	RH
754302	22	65	1hz	—	—	—	—	—	1	3	—	—	92	RH
740287	3	25	—	—	2	—	—	—	1	—	—	—	31	HR
734287	2	18	—	—	3	—	—	—	2	—	—	—	25	HR
663376	22	40	—	—	—	—	—	—	—	4	—	—	66	RH
673364	8	31	—	—	—	1	—	—	1	—	—	—	41	RH
676360	2	40	—	—	—	2	—	—	1	—	—	—	45	RH
682357	15	24	—	—	3	9	—	—	1	—	—	—	52	HR
682356	11	50	1hz	—	1	11	—	—	11	—	—	—	85	HR
683355	—	12	—	—	—	—	—	—	6	—	—	—	18	HR
683354	18	124	—	—	1	5	—	—	26	1	—	—	175	HR
677346	4	27	—	—	2	7	—	—	2	—	—	—	42	RH
679342	2	20	1	—	—	—	—	—	31	2	—	—	57	RH
675341	29	69	3hz	—	1	6	—	—	1	—	—	—	109	RH

* Ordinance Survey National Grid ST.

Table 7. Comparison of successive samples of *C. nemoralis* taken from the same locality. Data from the Berkshire Downs

map ref.	yellow			pink			brown	date
	00000	00300	12345	00000	00300	12345	00000	
SU 329827	74	105	20	90	31	4	4	Aug. 1960
	25	26	17	30	9	0	1	Mar. 1962
SU 331830	8	35	1	15	48	7	—	Aug. 1960
	9	32	3	13	37	5	—	Mar. 1962
SU 332831	24	81	1	11	41	3	—	Aug. 1960
	29	99	1	18	37	2	—	Mar. 1962
SU 333832	12	34	2	6	14	0	—	Aug. 1960
	32	93	10	16	59	3	—	Mar. 1962
SU 338836	6	60	34	1	24	10	—	Aug. 1960
	15	130	66	1	40	22	—	Mar. 1962
SU 338837	47	119	40	1	23	10	—	Aug. 1960
	17	131	33	3	32	11	—	Mar. 1962
SU 346852	44	69	3	5	18	4	—	Aug. 1960
	23	179	8	4	33	1	—	Mar. 1962

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TABLE 8. DISTRIBUTION OF VERY PALE, PALE AND DARK PINK *C. NEMORALIS* IN SAMPLES TAKEN FROM THE GORING DISTRICT OF THE BERKSHIRE DOWNS

map reference all SU	very pale pink	pale pink	dark pink	habitat
482812	—	10	—	O
482812	1	16	4	O
483875	2	4	—	O
483875	11	5	—	O
493823	—	1	—	O
495812	—	6	2	O
497885	2	8	4	O
508804	—	3	5	W
527807	1	7	—	O
530814	14	21	6	W
530814	10	19	1	W
544832	—	11	—	O
549841	6	—	—	O
550851	3	3	—	O
553845	—	16	1	O
556837	1	17	16	W
459812	10	15	5	O
562812	5	12	1	O
563812	3	5	1	O
564813	4	14	1	O
566837	—	1	—	O
566822	3	13	35	W
567817	2	13	38	W
568822	1	8	9	O
573802	4	3	1	O
573802	4	3	1	O
581801	—	16	—	O
582808	2	12	1	O
586801	4	8	22	O
587849	2	5	—	O
587806	7	12	6	O
588804	5	23	29	W
654777	—	3	—	O
588806	5	18	19	W
588804	—	12	25	W
589851	2	1	—	O
589811	3	8	1	O
589807	4	12	9	O
589806	—	11	10	O
589806	3	16	14	O
592803	—	11	10	W
617815	12	12	1	O
619795	7	14	—	O
617815	25	22	6	O
619792	1	6	6	W
619792	—	4	5	W
625849	4	5	—	O
626899	2	3	1	O

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Table 9. Numbers of light spread banded and dark spread banded *C. nemoralis* in samples from the Lambourn and Uffington districts on the Berkshire Downs

map ref.	light spread bandeds	heavy spread bandeds	habitat
292840	2	5	W
296850	2	8	O
297845	2	2	O
297837	5	6	O
297865	26	39	O
299866	21	22	O
300867	21	10	O
300863	8	3	O
301868	9	11	O
301830	1	9	O
302870	2	1	O
305858	9	13	O
307849	15	16	W
308858	2	4	W
308848	69	68	O
308844	8	16	O
309842	8	19	W
311865	13	29	W
315865	2	3	O
324835	3	5	W
325833	1	1	O
325860	10	48	W
326862	3	4	O
332831	4	23	W
332832	2	7	W
335858	2	8	O
338836	6	17	W
338837	8	30	W
339810	8	8	O
339810	10	20	W
339809	3	11	O
342811	8	3	O
344814	25	7	O
345835	24	5	O
348854	3	14	O
349835	4	26	O
355858	2	8	O
356853	15	37	W
358852	5	56	W
358859	3	2	O
359853	5	6	O
330829	9	6	O
354857	3	2	O
325855	3	9	O
346852	13	8	O
347853	1	2	O
333818	16	1	O
333856	1	3	W
343851	3	17	W
337834	4	1	W
336834	1	1	W
331830	3	11	W
333818	3	3	W
332827	3	9	W
331821	3	2	W
329827	3	1	O

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Table 10. Frequency of dark shells in samples of *C. nemoralis* from the Lambourn and Uffington districts of the Berkshire Downs

map ref.	brown	pink	heavy spread + yellow fusions	sample size	habitat
292840	3	92	8	166	W
293847	8	26	—	41	W
295834	3	18	1	64	O
296850	—	8	8	34	O
297845	3	2	2	28	O
297834	—	48	—	62	O
297837	—	2	—	70	O
297865	4	43	34	145	O
298834	—	1	—	34	O
299816	5	24	11	96	O
300867	—	19	9	81	O
300863	—	6	1	30	O
301868	7	64	9	106	O
301830	—	23	8	62	O
302870	—	21	2	32	O
303777	—	34	5	103	O
305858	—	11	13	49	O
307804	1	—	5	14	O
307849	—	17	18	95	W
308858	—	26	2	37	W
308869	4	7	—	22	W
308848	—	68	69	477	O
308844	—	1	17	73	O
309842	—	6	18	150	W
311865	1	19	39	143	W
311864	—	2	11	34	W
315865	—	3	11	35	O
320864	—	17	1	33	O
322858	—	22	—	36	O
323855	—	22	2	37	O
323855	—	19	4	31	O
324835	—	41	5	79	W
325851	—	4	—	31	O
325833	3	43	6	225	O
325841	—	—	1	23	W
325860	—	162	174	457	W
326841	—	5	5	39	O
326862	—	7	38	88	O
327843	—	1	—	71	O
331830	—	128	12	216	W
332831	—	112	231	348	W
333832	—	98	10	281	W
333856	—	—	11	77	W
334857	—	—	—	59	W
335858	—	—	2	101	O
338836	—	98	43	409	W
338837	—	80	59	487	W
339810	—	17	8	93	O
339810	—	70	15	160	W
339809	—	27	8	72	O
342811	—	6	2	50	O
344814	12	16	7	167	O
345847	—	—	22	114	O
345835	—	—	5	68	O
348854	—	53	27	190	O
348829	—	2	—	13	O
349855	—	93	40	366	O
349819	5	1	—	86	O

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TABLE 10 (*cont.*)

map ref.	brown	pink	heavy spread + yellow fusions	sample size	habitat
351852	—	—	1	36	O
355858	—	—	2	87	O
354853	—	—	7	70	O
356853	—	—	31	92	W
358818	—	50	4	123	W
358852	—	—	59	124	W
358859	—	—	2	18	O
359853	—	—	6	41	O
359860	—	—	—	19	O
329828	—	33	2	86	O
330829	3	16	6	74	O
354857	—	—	2	26	O
352855	—	10	11	102	O
346852	—	27	10	143	O
347853	—	3	3	25	O
333818	—	—	1	56	O
343851	—	57	9	77	W
341846	5	30	—	59	W
340844	2	18	2	41	W
338840	—	5	3	52	W
337834	—	36	6	120	W
336834	—	4	2	135	W
336833	—	1	5	211	W
333818	14	31	1	78	W
332827	76	161	14	305	W
331821	1	64	1	207	W
329827	1	39	4	108	O
332826	11	9	1	30	W

TABLE 11. FREQUENCIES OF YELLOW AND EFFECTIVELY UNBANDED *C. NEMORALIS* IN PAIRS OF SAMPLES FROM ADJACENT LOCALITIES IN THE UFFINGTON DISTRICT OF THE BERKSHIRE DOWNS

locality	map ref.	habitat	% Y	% E.U.
Pingoose Couvert.	293847	W	17	76
	297849	O	82	86
Compton Bottom	292840	W	43	46
	289843	O	49	38
Towers Hill	284844	W	71	41
	283843	O	97	8
Compton Beauchamp	281859	W	35	32
	280860	O	46	42
Odstone Hill	277856	W	27	37
	275856	O	72	0

TABLE 12. FREQUENCIES OF SAMPLES CONTAINING BROWN *C. NEMORALIS* IN ALL DISTRICTS ON THE BERKSHIRE DOWNS

	Liddington		Uffington		Lambourn		Wantage		Ilsley		Goring	
district	brown	non-brown	brown	non-brown	brown	non-brown	brown	non-brown	brown	non-brown	brown	non-brown
lower plain	—	—	—	—	1	2	5	6	4	1	8	2
scarp.	6	2	7	1	12	27	4	1	1	—	12	3
plateau	2	23	11	12	5	20	2	4	1	7	17	10
woods	—	9	4	1	11	29	8	5	4	1	12	6

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TABLE 13. DISTRIBUTION OF SAMPLES OF *C. HORTENSIS* CONTAINING PINK AND/OR BROWN MORPHS IN VARIOUS REGIONS OF ENGLAND THAT HAVE BEEN SURVEYED. OPEN HABITATS ONLY

region	no. of samples containing pinks/browns	total no. of samples
Oxford district	12	22
Berkshire Downs	30	171
Marlborough Downs	7	28
Salisbury Plain	17	46
Purbeck Hills	37	47
South-east Somerset	27	28
Kent*	36	37
Western South Downs†	18	31

* Data from Diver, unpublished.

† Data from Carter and Palles Clark, unpublished.

TABLE 14. COMPARISON OF MORPH FREQUENCIES IN A SUBFOSSIL SAMPLE WITH THOSE IN NEARBY PRESENT-DAY ONES. DATA FROM THE UFFINGTON DISTRICT OF THE BERKSHIRE DOWNS

Cepaea nemoralis

		00000	00300	12345	12345sp	total
subfossil sample	SU 281854	8	3	10	8	29
present-day samples	SU 286857	11	0	36	13	60
	SU 281859	26	2	63	0	91

C. hortensis

		00000	12345	fusions	total
subfossil sample	SU 281854	3	9	17	29
present-day samples	SU 283855	33	33	9	75
	SU 286856	35	14	0	49

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