PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Sand-Dune Populations of Cepaea nemoralis (L.)

A. J. Cain

Phil. Trans. R. Soc. Lond. B 1968 **253**, 499-517
doi: 10.1098/rstb.1968.0009

STUDIES ON *CEPAEA*

V. SAND-DUNE POPULATIONS OF *CEPAEA NEMORALIS* (L.)

By A. J. CAIN

Department of Zoology, University of Manchester

(*Communicated by P. M. Sheppard, F.R.S.—Received* 13 *February* 1967)

CONTENTS

A survey of duneland populations of the polymorphic snail *Cepaea nemoralis*, based on 170 samples from 53 localities on the British and Irish coasts, shows an overall distribution of morph frequencies consistent with the action of visual selection. Some geographical trends of variation can be discerned, but there is great variation, often over short distances within one group of dunes. A detailed investigation of this has been made at Point of Air, Flintshire. Here and at several other dune systems there is an association of the occurrence of dark browns with complex topography which suggests that they are favoured by very local climatic effects caused by the accumulation of cold air. If local temperature or other climatic factors is effective, the apparent agreement of duneland populations with what is expected as a result of visual selection may be misleading.

1. Introduction

Lamotte (1959), rejecting the view that visual selection (Cain & Sheppard 1954) is of importance in determining morph frequencies in *Cepaea*, suggests that climatic selection has great influence, favouring yellows and unbandeds in more open habitats such as meadows, and pinks and bandeds in woodlands. It is indeed likely that many different sorts of selection are acting on the various genes concerned in this polymorphism; and that some form of non-visual selection may be acting to maintain it was pointed out by Cain & Sheppard (1950, 1954). A study of duneland populations, which live in open sunny habitats (Manley 1952), is likely to throw light on the various factors influencing the polymorphism. The purpose of this paper is to present the results both of a general survey of British and Irish duneland populations and of an intensive survey of one group of duneland populations at Point of Air, Flintshire. While the general characteristics of all these populations are consistent with a considerable influence by visual selection, not by climatic selection in the directions suggested by Lamotte, there are some remarkable features best attributed to selection by climate, the influence of which may be pervasive.

2. General survey of duneland populations

Table 1 in the Appendix gives data on the composition of samples other than at Point of Air. Variation in frequency of the colour morphs is shown in figure 1 and of banding in figure 2. Figures 3 to 5 are scatter diagrams directly comparable with that given by Cain & Currey (1963) for the Oxford district, in which visual selection is effective. The present diagrams are for the British duneland populations except Point of Air, the Irish ones, and those on the Mullaghmore Peninsula reported by Cook & Peake (1962) respectively.

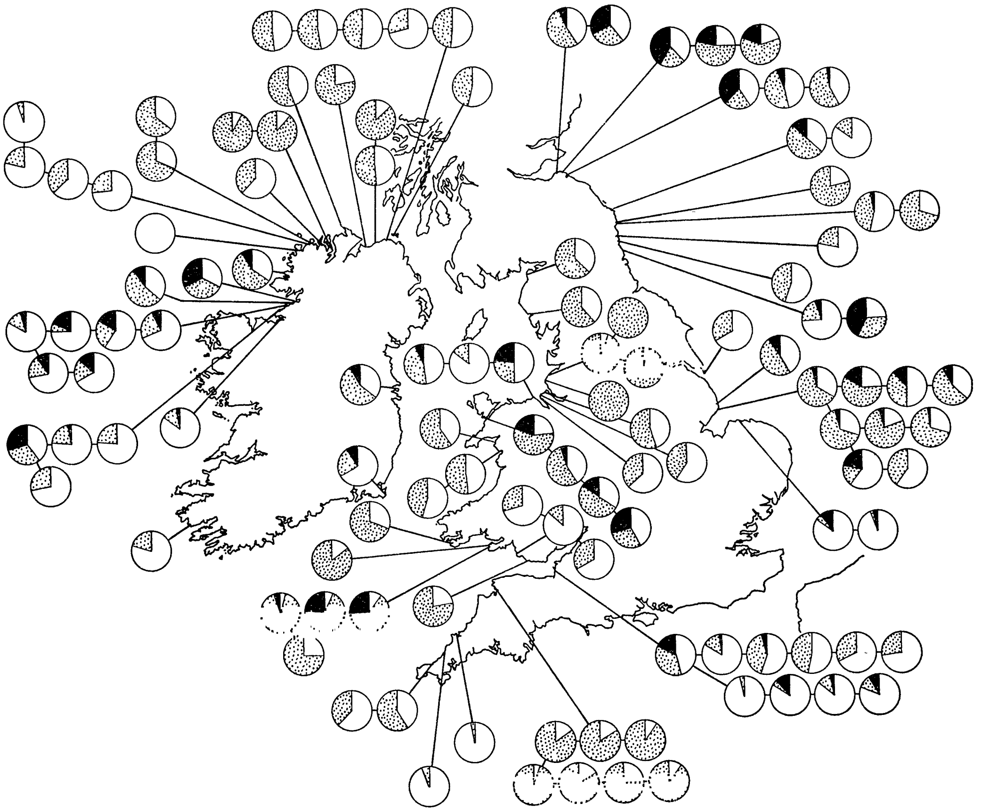

Figure 1. Frequencies of the principal colour morphs in samples from duneland. White = yellow, dotted = pink, black = all browns. Samples joined together are from the same duneland area. (Three samples from Point of Air are included.)

Figures 1 and 2 show immediately that yellows and pinks, varying greatly in relative proportions from place to place, are far commoner than brown shells, and that five-bandeds are overall much the commonest of the banding morphs. Table 1 shows that very few five-bandeds are effectively unbanded, i.e. with the top two bands (at least) missing; indeed, one is struck with the heavy and emphatic banding of the shells, pale or smudgy bands being very uncommon. Most of our samples are from marram grass (*Ammophila arenaria* (L.) Link) with some admixture of other grasses and herbs. Some (e.g. Ainsdale, Formby, Wallasey, some Berrow samples, Clashybawn 1 and 2, Tramore Strand 3 and 4) are from stabilized areas with short turf, and one (Meols) from long grass, but show little difference from the rest. In almost all duneland habitats (except where there are shrubs, as with the sea buckthorn *Hippophaë rhamnoides* L. on the south-east coast) the general

BIOLOGICAL SCIENCES THE ROYAL SOCIETY PHILOSOPHICAL TRANSACTIONS OF

background is noticeably stripy with stems and leaves of marram and other grasses, often rather wiry and with some dead straw-coloured material; in most marram there is some exposure of sand between the tufts. Direct matching of live snails shows that both yellows (with a faint to strong tinge of green when the shell is occupied) and pinks are a good match over most of the types of background, much better than reds or dark browns, though the latter may be overlooked when in the dark interspaces between clumps. Many of the pinks in the collections are medium, pale or faint pinks, but reds are not uncommon. Some of the samples are of thrush-broken material and it is possible that thrushes are present on duneland generally, but there is no information for most localities; experience at Point of Air shows that in such open habitats thrushes may be extremely wary and difficult to see, and the finding of freshly broken shells may be one's only indication of their presence.

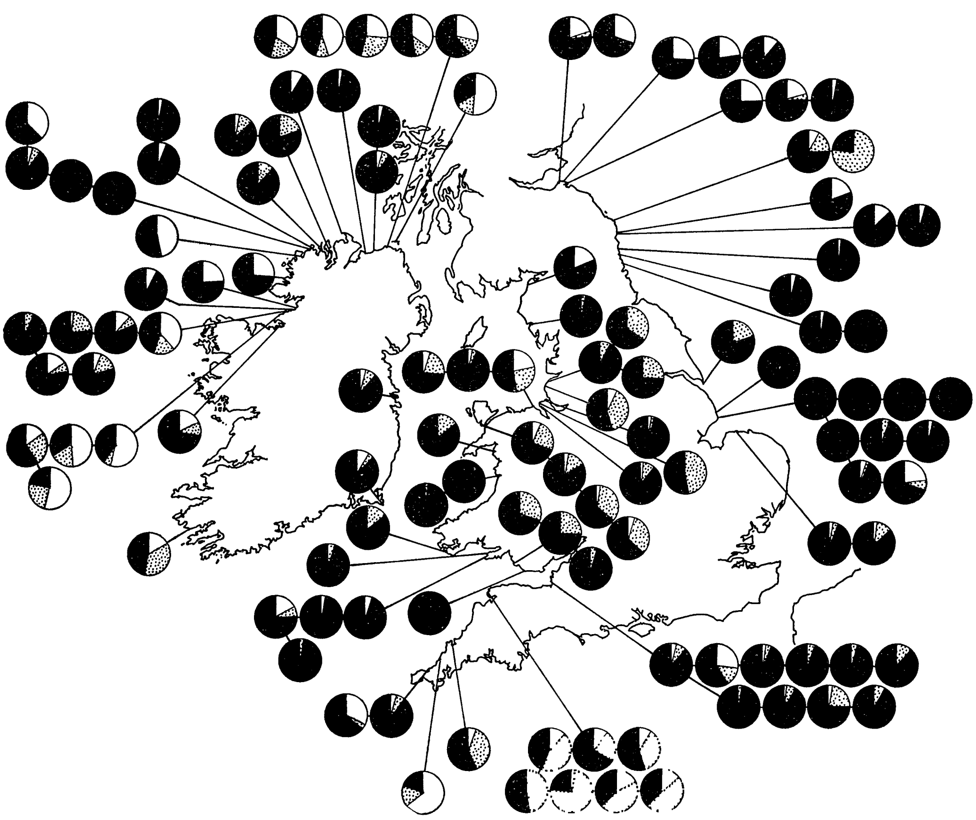

FIGURE 2. Frequencies of the principal banding morphs, in all colours except browns, in samples from duneland. White = 00000, dotted = 00300, black = all others (almost entirely 12345). Other conventions as in figure 1.

The scatter diagram (figure 3) for the British dunelands shows a complete range of possible values in relative proportions of pinks and yellows, fairly evenly scattered with some preponderance perhaps between 20 and 60 %, and a definite clustering into the lower values for effectively unbandeds, half the values being below 30 %. The scatter is clearly different from that for woodland in the Oxford district; it resembles more that for hedgerows and rough herbage in the same district but extends more uniformly over the range of colour, and approaches more closely towards 0 % effectively unbandeds. This is

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

what would be expected if visual selection by birds is operating, since the habitats in the Oxford district included under hedgerows and rough herbage have a far higher proportion of broad-leaved herbs than do duneland habitats generally, and of course they have no sand; the soil is usually dark with humus. The Irish dunelands (figure 4) while agreeing with the British ones in range of colour, show a general scatter in values of effectively unbandeds extending more frequently into the higher values; and this impression is strengthened when we consider the values for the populations reported by Cook & Peake (1962) for the Mullaghmore Peninsula, Co. Sligo, Eire (figure 5).

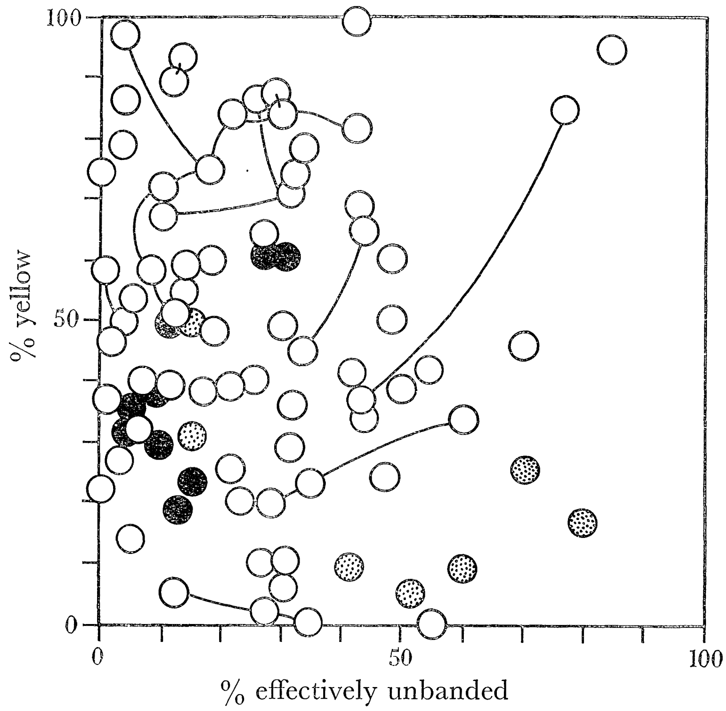

FIGURE 3. Scatter diagram for all samples from British dunelands except Point of Air, scored to estimate the effects of visual selection (compare Cain & Currey 1963*a*, fig. 7). Symbols joined by a line (not those merely adjacent or overlapping) or with the same shading except plain white are from the same duneland.

Figure 2 shows the proportions of the major banding forms in non-brown shells (since dark browns are normally unbanded). There seem to be definite regions in both Ireland and Britain which are characterizable on banding frequencies, even though there are often great variations between samples from the same locality. The Irish localities show overall a higher proportion of unbandeds than do the British overall, but the northern coast, except for the two most westerly localities (Rathlin Isle and Whitepark Bay) has very few unbandeds—one sample of the four from Tramore Strand has a high proportion. In Britain, unbandeds are at all frequent only in the north-east from Gullane to Alnmouth and in two of the four Cornish samples. Mid-bandeds in Ireland are scarce or absent over a wider stretch of coast than unbandeds, extending in the west to Bundoran but with exceptions at Lough Swilly and Sheephaven. In Britain they are scarce or absent, except for three samples, along the whole east coast, the Lake District coast (if two samples are a guide) and most of the west and south Welsh coast. They are conspicuous only in

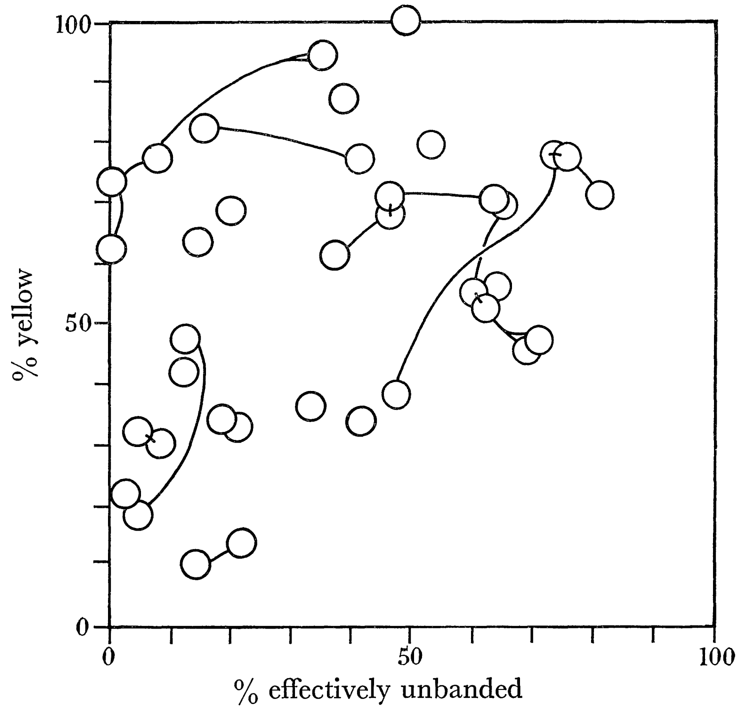

FIGURE 4. Scatter diagram as in figure 3 but for Irish dunelands.

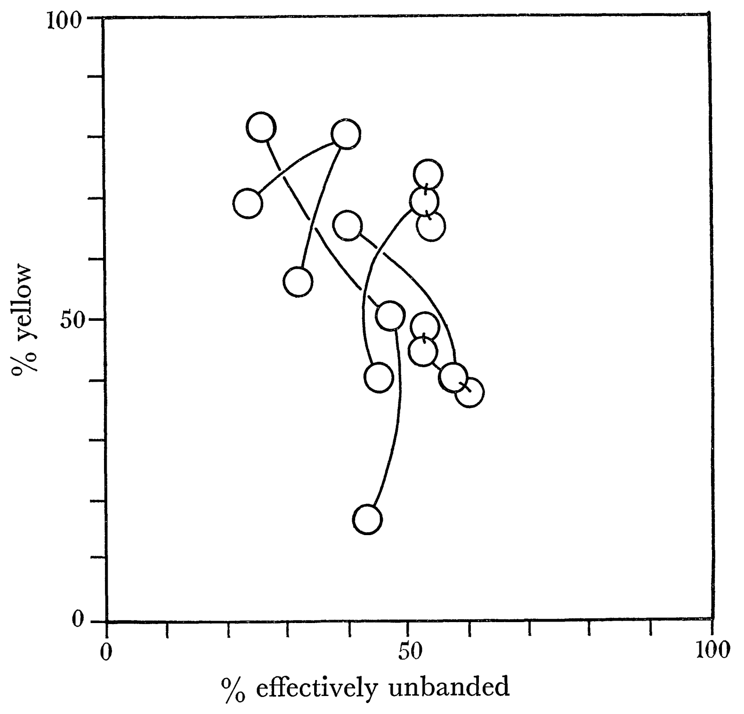

FIGURE 5. Scatter diagram as in figure 3 for the samples reported by Cook & Peake (1962) for the Mullaghmore Peninsula, Co. Sligo, Eire.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Lancashire and on the north Welsh coast (including Anglesey), and in the extreme south-west at Braunton and Crantock. Kenfig (South Wales) also has a high proportion in two out of three samples.

3. The Point of Air populations

Table 2 gives data for the samples and figure 6 is the corresponding scatter diagram, Figure 7 shows the geographical variation in morph frequencies for both colour and banding, and figure 8 gives details of the topography and collecting areas. The general aspect of the samples agrees with that from other duneland localities in Britain (figure 3), but high values of pinks are much less common. Most of the samples form a fairly compact cluster in the diagram, more compact than those from a single habitat-class of similar nature—e.g. rough herbage—in the Oxford district (Cain & Currey 1963, figure 7).

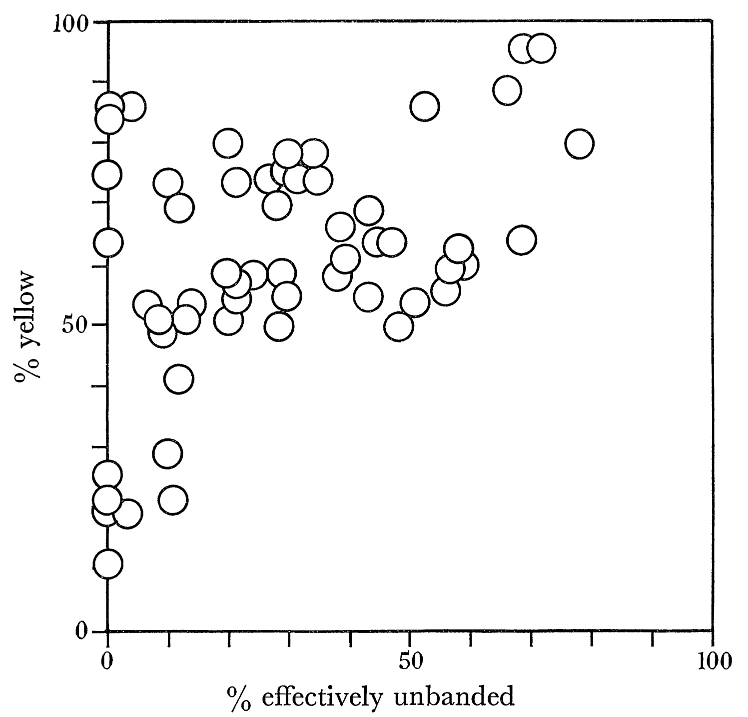

Figure 6. Scatter diagram as in figure 3 for all samples from Point of Air.

This is not surprising if visual selection is effective, since the variation in character of the background at Point of Air is slight. Samples from other single dune-systems also tend to cluster (figures 3 to 5) but their means show a wide scatter, too wide considering the similarity of the background on most of the dunelands. Moreover, some samples at Point of Air depart widely from the rest, and the morph frequencies show a remarkable geographical distribution (figure 7). Unbandeds (in pinks and yellows) are almost confined to the westernmost quarter, and reach 14 % at one station there (25). Browns are absent from the eastern third, rise to remarkable frequencies in the central third (31 % at 12, 30 % at 17) and occur in part of the western third at low frequencies (1 to 6 %). Mid-bandeds also vary remarkably, reaching 70 to 78 % at 40 and 41, and 64 % at 18. Yellows are abundant at most stations except right in the middle. Changes in frequency from one collecting station to the next are sometimes abrupt—e.g. 35 stands out from 34 in its high percentage of pinks

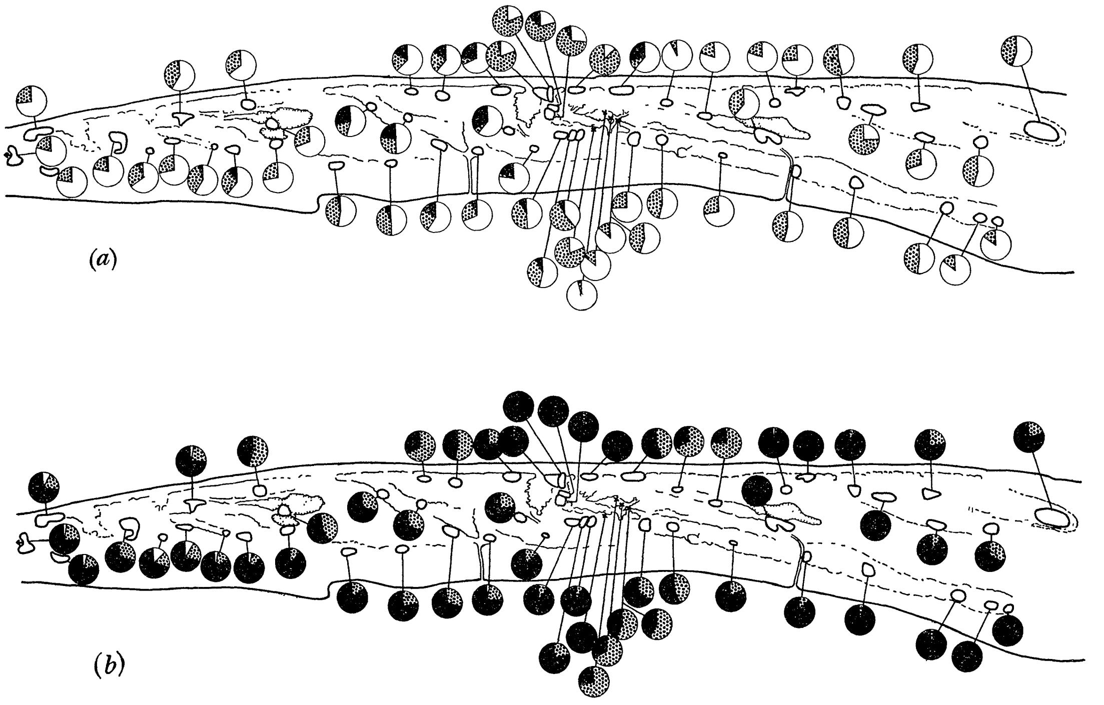

FIGURE 7. Geographical variation in morph frequencies on the sand-dunes at Point of Air in (*a*) colour and (*b*) banding (non-browns); conventions as in figures 1 and 2. Outlines of the principal dunes and two wet-slack areas (dotted) shown for comparison with figure 8.

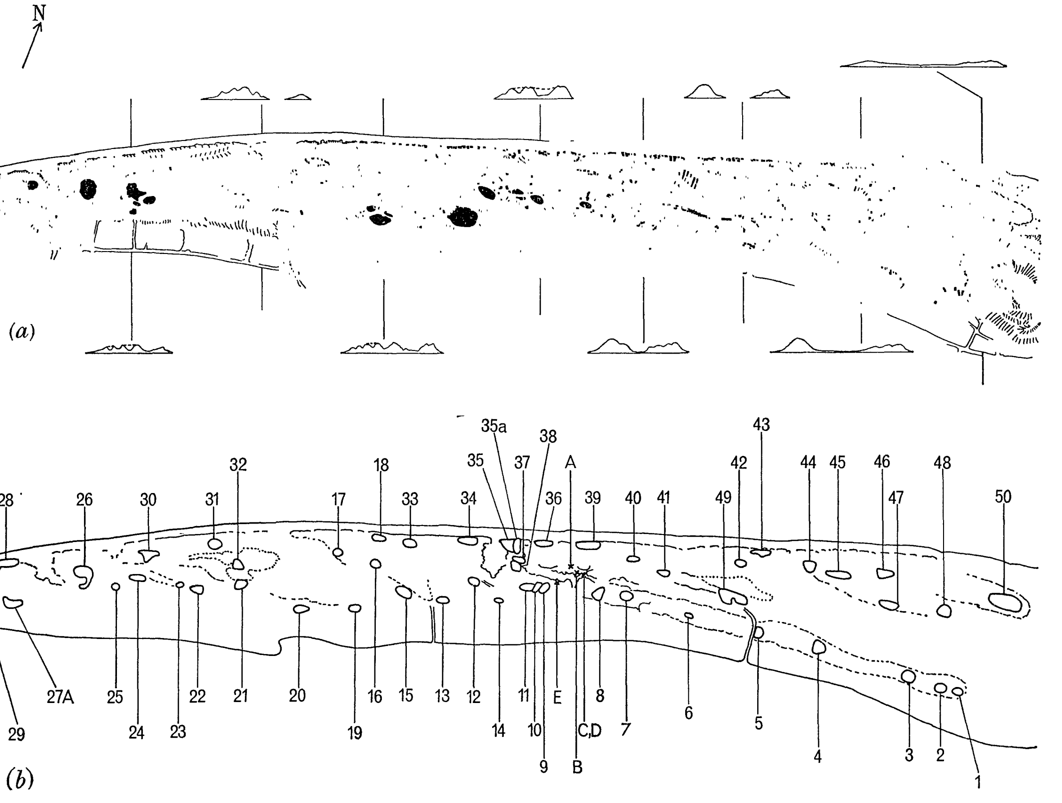

FIGURE 8. Topography of the Point of Air dunes. (*a*) Major features only of the dunes. Stippled areas, flats. Duneland slopes hachured. Pits and smaller enclosed areas black. In the cross-sections, the plan is correct but the elevation only sketched, height exaggerated. Absence of the baseline indicates a wet slack (with no *Cepaea*). Dots complete the lip of a pit or amphitheatre. (*b*) Location of our samples for comparison with the topographical map above.

and five-bandeds. In fact, although the locus for mid-banded is unlinked to those for colour and for unbandeds versus bandeds, there is a considerable and abrupt 'area effect' (Cain & Currey 1963*a*—if the name can be applied to so small an area) involving high frequencies of yellows and mid-bandeds (stations 7, 8, A, B, C, D, 39, 40, 41) stretching right across the dune systems and sharply juxtaposed to another of pinks and five-bandeds (stations E, 9, 10, 11, 35, 35A, 36, 37, 38). The collections A, B, C, D, E were made to investigate the edge of the first mentioned area effect.

Figure 8 shows the stations in relation to the general topography of the dunes. The peculiarities of morph frequency are related neither to the variations in habitat (from flat, often wet, slacks with short turf to loose sand with pioneer marram on the seaward slopes) nor to particular dune ridges, which might differ from one another in age. This lack of correspondence with obvious ecological features was remarked on many years ago by Captain Diver after surveying the dunes at Berrow and Bundoran in great detail, and the present observations confirm his. There is, however, a general association at Point of Air between variation in morph frequencies and the complexity of the topography. As figure 8 shows, the eastern quarter of the duneland is of very simple topography, with a low seaward dune area sloping down into a wide flat space with relict dune ridges only 5 to 10 ft. high; this big flat is abruptly terminated to the south by the high but simple line of landward dunes. In the next quarter the width of the duneland decreases, and the seaward dunes become steeper and more complex, consisting of several ridges more or less coalescing. As the landward dunes approach the seaward dunes, the flat is narrowed, and partly broken by subsidiary dunes, never as high as those of the main ridges and ending without meeting the landward dunes. In the centre of the survey areas, a far greater complexity of structure is found. The landward and seaward systems are joined by a very high and steep cross-dune; the flat to the east of it is the bottom of a great amphitheatre with only a narrow defile a few feet wide connecting it to the big eastern flat; and the landward dunes enclose several deep pits, some 20 ft. deep and 40 yd. across, others shallower. Some of these pits seem to be formed by a cross-dune moving to and blocking a steep-sided valley. Others of more circular shape are probably blow-outs overgrown with marram. In the third quarter the landward dunes remain complex with pits, and oblique complex systems run towards and join the high seaward dunes, which have been breached by a large and active blowout just west of the big cross-dune forming the western wall of the ampitheatre described above. An older blow-out has removed the seaward dunes on the border between this quarter and the westernmost and a large flat, with fresh water, is open towards the sea. In the westernmost quarter one can hardly distinguish the seaward from the landward dunes; there is considerable complexity, with pits here and there, on the landward side, but the seaward edge is low with many gaps.

Comparing figures 7 and 8 we see that the easternmost quarter has the simplest structure and the simplest variation in morph frequencies. The most complex structure is in the central half, and there occur the two area effects described above, and almost all the dark browns. The westernmost quarter is intermediate in complexity. The seaward parts are simple and with morph frequencies like those of the easternmost quarter; the landward parts are complex and browns occur sporadically, also a few unbanded (virtually absent elsewhere) in the most pitted area. The comparison suggests, then, that there is some relation between complexity of variation and of topography, and especially that the greatest complexity in variation is associated with the greatest development of enclosed spaces (pits and amphitheatres).

4. Topography and dark browns

Two distinct sorts of browns can be found on duneland. One is the usual dark to medium brown, widely scattered in other habitats in the British Isles, and remarkable in that it is nearly always unbanded, even when yellows and pinks from the same population are heavily banded (e.g. Cain & Sheppard 1954). The other, distinguished by Diver and subsequently by Clarke & Murray (1962*a*) at Berrow is much paler, often with only a flush of brown, and is not conspicuously less banded in any sample than the yellows and pinks. Most of the banded browns in table 1 are pale browns. Little is known about the distribution of pale browns, but Cain & Currey (1963) have given reasons for expecting that dark browns may be associated with places subject to cooling by the accumulation of cold air, which is a frequent process on calm nights in Britain. Carter (1965 and this volume) has provided further evidence for this from a much more widespread survey of high downland than Cain & Currey's. Accumulation of cold air is marked in valleys in open rolling country, especially grassland, with few obstacles such as hedges to the air flow (Geiger 1959). In this respect, downs and dunes have much in common.

All the browns at Point of Air, except one individual, are dark browns, and as shown in the previous section, they are largely associated with complex areas of duneland containing pits or large enclosed areas, structurally capable of retaining cold air. An exact correspondence can hardly be expected in the diagrams since only the major complexities are shown, and since dunes are unstable; the apparent exception of stations 33 and 34 may be due to shallow depressions or to the recency of opening of the blow-out west of the main cross-dune. Nevertheless, of 20 occurrences of dark browns at a frequency higher than 2% at Point of Air, 12 are definitely associated with pits and enclosed spaces, six are in complex areas which may well accumulate cold air, and only two appear exceptional, which are associated with an active and probably recent blow-out.

The general correspondence in complexity of variation and of dune topography was commented on during the surveys (by myself and Professor P. M. Sheppard, F.R.S.) on the ground at Point of Air. The specific hypothesis of an association between the accumulation of cold air and occurrence of dark browns was suggested on a visit (by A.J.C.) to Newborough Warren, Anglesey, where in parts of the dune area away from the sea dark browns are common and the topography is complex with large and extensive enclosed areas. Dr P. O'Donald, who is surveying populations of *C. nemoralis* in the Nature Conservancy reserve at Newborough Warren, tells me that dark browns are absent near the sea where the topography is much simpler.

A preliminary survey to test the hypothesis has been carried out at Gibraltar Point on the east coast of England, over a much smaller area than at Point of Air. Barnes & King (1952) give a survey of the dunes as part of an investigation of coastal development, and Chesters (1951) discusses some aspects of the vegetation. The topography is different from that at Point of Air, with two dune systems separated by an extensive salt-marsh, which narrows to the north where the dunes coalesce and is largely blocked to the south by a storm-beach where it opens into the Wash. Of the two dune systems only the landward one was in existence in 1824, and the marsh and the seaward complex are younger; the major ridge in the seaward complex (up to 30 ft. high) appears to have been the termination in 1904, and dunes to the east (seaward) of it are younger still. (One is forming at the present well out on the beach with an embryo saltmarsh landward of it.) Barnes & King give a general map and profiles but a detailed map of only a small area near the Point, at the south-eastern end. This, however, shows well the general structure of the seaward complex, namely long and rather uniform dune ridges of varying height, roughly parallel to the beach but curving gently to meet each other. The dips between them are very long and shallow, and vary greatly in width. They cannot be called pits; they are shallow depressions 20 to (in the main depression) 400 ft. wide, 10 to (exceptionally) 20 ft. deep, and up to a quarter of a mile long, usually pointed at both ends. The landward complex consists of only two large dune ridges, with a depression in between, itself subdivided in some places by a minor median ridge.

The saltmarsh between the dune complexes is of course low-lying and largely enclosed by the dunes and the storm-beach. The land behind the whole area is low marshy farmland. Cold air will certainly accumulate in the marsh and on the farmland, and the long depressions in the dunes should hold a shallow layer also. As the topography is not as accentuated as at Point of Air, one would expect that dark browns would occur, but probably at rather low frequencies throughout, except on the seaward face of the newer dunes, and on the prolongation southward of the landward dunes by the biological station; this last is low and flat sand, overgrown with turf, completely open to the sea southwards. No *Cepaea* could be found on the seaward face which is steep with very loose sand, and any snails found on it might well have rolled down from the depressions just behind. Nine samples of more than 30 shells were collected at various points (table 1). All had low frequencies of dark brown except one, a sample of 66 shells taken on the low ground by the biological station. The results of this, then, seem to support the hypothesis.

A number of other dune systems have also been visited personally. The results for the areas in them actually seen—none were completely surveyed—are as follows, where + signifies the presence of dark browns, – their absence, and a blank means that no duneland of that type of structure was visited in the locality (but may or may not occur somewhere there). The surveyed areas have been added:

locality	simple structure		enclosed areas present
Gibraltar Point	–		+
Silloth	–		
Ainsdale	–		
Formby	–		
Wallasey	–		
Hoylake	–		
Meols	–		
Point of Air	–		+
Newborough Warren			+
Llangennith	–		+
Kenfig	–		+
Merthyr Mawr		+	
Berrow	–	+	+
Gwithian	–		

To these areas may be added the following, from personal communication and other descriptions by competent observers.

Bamburgh	–			+
Seaton Point	–			
Alnmouth	–			
Druridge Bay	–			
Cresswell	–			
Seaton Sluice	–			
Spurn Head	–			
Braunton Burrows	–			
Streedagh	–			+
Newborough Warren	–			
	(–)	(+)	(–)	(+)
totals	22	2	0	8

The association of dark browns with complex structures is strong. There are only two apparent exceptions. At Merthyr Mawr the area visited consists of very high and steep dunes, certainly capable of producing and shedding downwards cold air, but with narrow valleys between leading rather directly to the sea. Accumulation seems likely to only a limited degree, and in fact the browns are a single individual in a sample of 118. At Berrow there appear to be no dark browns on the present seaward dunes, which are simple in structure, and they occur principally on the high middle dune system, which is complex. But a few also occur on the low sandy areas between the high dunes and the hinterland, which, as at Point of Air and Gibraltar Point, is low farmland, quite likely to accumulate cold air which could abut on the dunes. These occurrences at Berrow may not therefore really be exceptional, but are so listed here as being least favourable to the hypothesis; two occurrences at the head of the little inlet do seem exceptional. Kenfig, Braunton Burrows, Ainsdale and Formby are classed as of simple topography here, although large areas with much physiographical and ecological complexity. The part of Kenfig visited was wide, rolling and nowhere of great elevation. The slacks were widely exposed, and run-off of cold air towards the sea seemed likely. Braunton Burrows is tentatively given the same classification in the tables as Kenfig for the same reasons, on the basis of descriptions by others, and photographs by Professor M. H. Williamson. The photograph in Salisbury (1952) is unlocalized but gives some indication of the topography. However, descriptions mention some projecting spurs from the main ridge (Steers 1946) and there may be some enclosed areas locally.

5. Discussion

On unstable dunes it may well be that some variation in morph frequencies is due to chance events; but that this cannot be taken as generally the case on stabilized ones has been shown by Clarke & Murray (1962*a*, *b*) from their repeat of the careful survey made at Berrow by Captain C. Diver and the late Professor Boycott. Clarke & Murray found that although the pattern of variation in morph frequencies bore no obvious relation to habitat, it had been maintained over 30 years, which is improbable without selection, and further, that two morphs showed overall changes in frequency suggesting mean selective values of about 6%, which is large; dark browns showed a general decrease and

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

mid-bandeds a general increase. It would be unwise to dismiss any of the variations shown in the present paper as merely random.

If as suggested above a complexity of frequency-variation is associated with a complexity of dune topography, and in particular dark browns are associated with enclosed areas capable of accumulating cold air, Diver's observation is partly explained; the association is with enclosed areas as such, not with obvious variations in habitat, which on duneland are primarily determined by the time at which an area of sand was last disturbed and the proximity of the water-table to the surface; equally there will be no association with simple altitude. But if temperature is important, it can act in many ways and at different times (mean day or night temperature of the surface, or extreme temperatures by day or night for example), and will be affected by aspect, at least during the day, as J. J. D. Greenwood has emphasized to me. The pink five-banded area at Point of Air is largely on steep eastern and north-eastern faces, while the yellow mid-banded one is on broader slopes trending south-west and little able to shade one another. More detailed surveys of duneland with strongly marked topography are needed before conclusions can be reached, but a comparison with open downland is interesting. Yellows and mid-bandeds are characteristic of much (but not all) of the higher barer downlands of the Marlborough and Lambourn Downs, while five-bandeds are abundant on the northeast-facing scarps associated with them (Cain & Currey 1963). At the present, five-bandeds occur in the lowlands just west of the Marlborough Downs, but in the Neolithic and Bronze Ages, when the climate was warmer and drier, the whole district seems to have carried only unbandeds and a few mid-bandeds (Currey & Cain, this volume, p. 492). Extensive areas of five-bandeds are reported by Carter (this volume, p. 412) from downland just east of the Marlborough Downs, but much of this downland is less high than the Marlborough Downs and on the highest point (Liddington Castle) there is a population with a high proportion of mid-bandeds (Cain & Currey 1963, table 4). If the higher downs are warmer by shedding cold air downwards and in part by reason of extensive south-west-facing slopes, it is perhaps not surprising that yellows and mid-bandeds are commoner there, since they are frequent in France in open country generally (Lamotte 1954, 1959). Large areas of five-bandeds are also reported by Arnold (1966) on the South Downs, but these downs have a remarkably maritime climate, mild and damp, as can readily be seen from many of the plant distributions in the *Atlas of the British Flora* (Perring & Walters 1962) and the maps of humidity, February minimum, and January and July means provided in it. Now dunelands all round the British coasts have much in common climatically and in fact the scatter diagrams in the present paper show that the samples reported here for Britain, although so scattered in distribution, show rather less heterogeneity than do those of the Oxford district and far less than those of the Marlborough Downs (Cain & Currey 1963, figs. 7 and 9 to 11), districts minute in extent by comparison. If the climatic conditions of dunes in general are such as to favour an abundance of five-bandeds and plenty of pinks, the apparent agreement of the scatter diagrams with what might be expected from visual selection may be partly or wholly coincidental; only experiment can settle the question.

If climatic factors are effective in influencing morph frequencies on the dunes, then the greatest variation in the morphs most readily affected by it will be with strongly marked topography. The lack of correspondence between banding morphs and general climatic variation in Brittany found by Guerrucci-Henrion (1966) may perhaps be due to great variation with topography. There may also be general trends from region to region, associated with general climatic variation over the British Isles—the difference seen in the Irish samples as compared with the British (figures 3 to 5) may be an example. Guerrucci-Henrion (1966) has shown such a dependence in Brittany between yellow and a maritime climate. However, there may be differences over considerable distances due mainly to topography, not general climatic variation. For example, many of the samples from the northern Irish coast come from shores running north and south along narrow sea-lochs, while those from the north-west coast are from north-west or west-facing shores, often transversely placed across the heads of west-facing bays. If the former shores carry simple long dune ridges parallel with the coast while the direct force of the westerly winds piles up complex ridges in the latter, a general difference in morph frequencies may be expected from dune topography alone.

Lamotte (1959) dismissed visual selection as unimportant and believes that climatic selection, much more constantly acting, can account for both general trends of variation from province to province in France and for the differences between populations sheltered in woods and those exposed in open habitats. Visual selection has now been demonstrated in the Oxford district and nearby by several authors (Sheppard 1951; Cain & Sheppard 1954; Murray 1962; Carter 1965; Arnold 1966, and in preparation) and the evidence for it cannot be simply dismissed, nor is it in any sense destroyed by the discovery of area effects elsewhere as Guerrucci-Henrion (1966) seems to believe. Moreover, it is clear from the present survey that in Britain, being situated in open habitats does not as such produce a high frequency of unbandeds and mid-bandeds and yellows, as Lamotte would expect. Further, the association he finds in France with habitat (1959) is of pinks and five-bandeds with woods, yellows and less banded shells with open habitats; that in the Oxford district (Cain & Sheppard 1954) is of pinks and less banded shells in woods, yellows and five-bandeds being more prevalent in rough herbage, grassland and other open habitats, as one would expect from visual selection. The same association was found by Currey, Arnold & Carter (1964) in south Warwickshire, and is not that expected by Lamotte. Nevertheless, even in the much more generally cool, humid and maritime climate of Britain (as compared with most of France) climatic selection may well have a distinct effect, especially in the more extreme habitats or regions. The highest and most open downland, well away from the coast, is likely to have the most continental climate, and seems to carry appropriate morph frequencies at least in some areas. Duneland may be very maritime and again have morph frequencies more determined by climate. But in districts and habitats intermediate in character, such as the Oxford district, climatic selection may be less strong and visual selection can override its effects.

I am especially indebted to Professor P. M. Sheppard, F.R.S., for his help in the earlier stages of this work; the Point of Air survey and most of the collecting in Lancashire and Cheshire was joint work. I am further indebted to him for criticism of this paper in typescript. Many people have collected samples for this survey or allowed me to use scores of material in their possession; I must mention particularly Dr A. Comfort, Dr C. B. Goodhart, Miss H. Johnstone (Mrs Ives), Mr J. Cadbury, Mr C. Fairhurst, Dr C. B. Goodhart, Mr G. Lewis, Mr D. P. T. Burke and Dr and Mrs T. Parkin. Dr B. C. Clarke let me work through the original notes and scores of his survey with Professor J. J. Murray at Berrow, and Dr L. M. Cook gave further information on his and Mr Peake's collections from the Mullaghmore Peninsular. At the beginning of this survey, work on *Cepaea* was partly supported at Oxford by a grant to me from the Nuffield Foundation. The bulk of it has been supported by D.S.I.R. (now S.R.C.) as part of a programme directed by myself in functional systematics. To both these bodies my grateful thanks are due.

References

Arnold, R. W. 1966 Factors affecting gene-frequencies in British and Continental populations of *Cepaea*. D.Phil. Thesis, University of Oxford.

Barnes, F. A. & King, C. A. M. 1952 A preliminary survey of Gibraltar Point, Lincolnshire. *Bird Observatory and Field Research Station, Gibraltar Point, Lincolnshire, Report for* 1951, pp. 41–59.

Cain, A. J. & Currey, J. D. 1963 Area effects in *Cepaea*. *Phil. Trans.* B **246**, 1–81.

Cain, A. J. & Sheppard, P. M. 1950 Selection in the polymorphic land snail *Cepaea nemoralis*. *Heredity* **4**, 275–294.

Cain, A. J. & Sheppard, P. M. 1954 Natural selection in *Cepaea*. *Genetics* **39**, 89–116.

Carter, M. A. 1965 An investigation of the area effects in *Cepaea*. D.Phil. Thesis, University of Oxford.

Carter, M. A. 1968 Studies on *Cepaea*. II. Area effects and visual selection in *Cepaea nemoralis* (L.) and *Cepaea hortensis*. *Phil. Trans.* B **253**, 397–446.

Chesters, C. G. C. 1951 A preliminary account of the vegetation of the foreshore from Seacroft to Gibraltar Point. *Bird Observatory and Field Study Centre Gibraltar Point, Lincolnshire, Report for* 1950, pp. 48–57.

Clarke, B. C. & Murray, J. J. 1962*a* Changes of gene frequency in *Cepaea nemoralis* (L.). *Heredity* **17**, 445–465.

Clarke, B. C. & Murray, J. J. 1962*b* Changes of gene frequency in *Cepaea nemoralis* (L.): the estimation of selective values. *Heredity* **17**, 467–476.

Cook, L. M. & Peake, J. F. 1962 Populations of *Cepaea nemoralis* L. from sand-dunes on the Mullaghmore Peninsula, Co. Sligo, Ireland; with a comparison with those from Annacoona, Dartry Mts., Co. Sligo. *Proc. Malac. Soc. Lond.* **35**, 7–13.

Currey, J. D., Arnold, R. W. & Carter, M. A. 1964 Further examples of variation of populations of *Cepaea nemoralis* with habitat. *Evolution* **18**, 111–117.

Currey, J. D. & Cain, A. J. 1968 Studies on *Cepaea*. IV. Climate and selection of banding morphs in *Cepaea* from the climatic optimum to the present day. *Phil. Trans.* B **253**, 483–498.

Geiger, R. 1959 *The climate near the ground*. Cambridge, Mass.: Harvard University Press.

Guerrucci-Henrion, M.-A. 1966 Recherches sur les populations naturelles de *Cepaea nemoralis* en Bretagne. *Arch. zool. exp. gén.* **107**, 369–417.

Lamotte, M. 1954 Distribution en France des divers systèmes de bandes chez *Cepaea nemoralis* L. *J. Conch., Paris*, **94**, 125–147.

Lamotte, M. 1959 Polymorphism of natural populations of *Cepaea nemoralis*. *Cold Spr. Harb. Symp. Quant. Biol.* **24**, 65–84.

Manley, G. 1952 *Climate and the British scene*. London: Collins.

Murray, J. J. 1962 Factors affecting gene-frequencies in some populations of *Cepaea*. D.Phil. Thesis, University of Oxford.

Perring, F. J. & Walters, S. M. (eds.) 1962 *Atlas of the British flora*. London: Nelson.

Salisbury, E. J. 1952 *Downs and dunes. Their plant life and its environment*. London: Bell.

Sheppard, P. M. 1951 Fluctuations in the selective value of certain phenotypes in the polymorphic land snail *Cepaea nemoralis* (L.). *Heredity* **5**, 125–134.

Steers, J. A. 1948 *The coastline of England and Wales*. Cambridge University Press.

BIOLOGICAL SCIENCES
THE ROYAL SOCIETY
PHILOSOPHICAL TRANSACTIONS OF

Appendix

Table 1. Scores of samples of *Cepaea nemoralis* from British and Irish sand-dunes

locality		total	yellows 0	yellows 3	yellows 5	yellows 5E.U.	pinks 0	pinks 3	pinks 5	pinks 5E.U.	browns 0	browns 3	browns 5	browns 5E.U.
East Scotland														
Gullane	1	66	4	—	22	—	4	3	30	—	3	—	—	—
	2	648	46	—	222	1	89	—	72	—	139	—	79	—
N. Berwick	1	132	14	—	31	—	3	—	22	—	62	—	—	—
	2	158	17	—	20	—	2	—	82	—	36	—	1	—
	3	86	5	—	12	—	2	—	50	—	17	—	—	—
Tyningham	1	32	2	—	10	—	3	—	6	—	11	—	—	—
	2	33	—	2	13	—	5	—	10	—	3	—	—	—
	3	42	1	—	16	—	—	—	23	—	2	—	—	—
N.E. England														
Bamburgh	1	122	—	7	26	12	9	9	42	—	17	—	—	—
	2	26	—	17	5	—	—	3	1	—	—	—	—	—
Seaton Point		30	1	—	3	2	4	—	20	—	—	—	—	—
Alnmouth	1	104	11	—	44	1	3	—	41	2	2	—	—	—
	2	97	2	—	29	—	3	—	62	1	—	—	—	—
Druridge Bay		59	2	—	44	—	—	—	13	—	—	—	—	—
Cresswell		487	20	—	237	—	5	—	225	—	—	—	—	—
Seaton Sluice	1	192	1	—	142	—	—	—	38	—	—	—	11	—
	2	76	—	—	20	—	—	—	24	—	9	—	15	8
East England														
Spurn Head		51	—	5	24	4	—	4	13	1	—	—	—	—
near Skegness		36	—	—	14	—	—	—	18	—	4	—	—	—
Gibraltar Point	1	46	—	—	16	—	—	—	28	—	2	—	—	—
	2	47	—	—	11	—	—	—	29	—	7	—	—	—
	3	59	—	—	29	—	—	—	23	—	7	—	—	—
	4	52	—	—	19	1	—	—	28	—	4	—	—	—
	5	44	—	—	14	—	—	—	28	—	2	—	—	—
	6	32	—	—	6	—	—	2	22	—	2	—	—	—
	7	31	—	1	7	1	—	—	21	—	1	—	—	—
	8	69	3	1	38	—	—	1	12	1	13	—	—	—
	9	66	12	4	24	—	2	1	22	1	—	—	—	—
Scolt Head	1	170	3	10	134	3	—	—	2	—	4	—	14	—
	2	416	5	45	336	1	—	1	6	—	1	1	20	—

Appendix

Table 1 (*cont.*)

locality		total	yellows 0	yellows 3	yellows 5	yellows 5 E.U.	pinks 0	pinks 3	pinks 5	pinks 5 E.U.	browns 0	browns 3	browns 5	browns 5 E.U.
N.W. England														
Silloth		24	3	—	6	—	1	—	14	—	—	—	—	—
Ravenglass		270	—	—	99	—	—	3	168	—	—	—	—	—
Ainsdale	1	131	—	—	6	—	—	16	109	—	—	—	—	—
	2	23	—	—	—	—	—	8	15	—	—	—	—	—
	3	79	—	—	1	—	—	22	56	—	—	—	—	—
Formby		159	—	—	—	—	11	62	71	15	—	—	—	—
Wallasey		241	1	—	112	—	1	2	125	—	—	—	—	—
Hoylake		33	—	9	10	1	—	6	7	—	—	—	—	—
Meols		152	2	13	75	—	—	6	56	—	—	—	—	—
N. Wales														
Newborough Warren	1	72	1	3	12	1	1	11	26	—	17	—	—	—
	2	273	—	26	82	2	1	24	124	1	13	—	—	—
	3	66	1	6	16	—	—	13	21	—	9	—	—	—
	4	66	2	10	16	—	—	3	14	—	17	3	—	1
Morfa Harlech		129	—	10	30	6	—	13	59	11	—	—	—	—
Morfa Dyffryn	1	65	—	—	30	2	—	—	33	—	—	—	—	—
	2	200	—	—	116	—	—	1	82	1	—	—	—	—
S. Wales														
Freshwater West		48	—	1	10	3	—	7	23	4	—	—	—	—
Llangennith Burrows	1	49	—	—	5	—	2	—	29	—	13	—	—	—
	2	41	—	—	4	—	1	—	26	—	10	—	—	—
	3	79	—	1	4	—	11	5	51	1	6	—	—	—
	4	71	—	1	18	—	—	1	51	—	—	—	—	—
Broughton Bay		320	—	4	39	—	—	9	266	2	—	—	—	—
Kenfig	1	35	—	8	17	—	—	3	7	—	—	—	—	—
	2	135	—	32	83	2	—	2	16	—	—	—	—	—
	3	67	—	3	39	3	—	1	21	—	—	—	—	—
Merthyr Mawr		118	—	—	26	—	—	—	91	—	1	—	—	—

APPENDIX

TABLE 1 (*cont.*)

locality		total	yellows 0	yellows 3	yellows 5	yellows 5 E.U.	pinks 0	pinks 3	pinks 5	pinks 5 E.U.	browns 0	browns 3	browns 5	browns 5 E.U.
S.W. ENGLAND														
Berrow	B 29	290	1	18	117	4	2	8	86	4	13	2	32	3
	B 33	159	46	12	72	1	3	2	16	—	1	2	4	—
	B 43	283	—	8	150	6	1	3	108	4	—	—	3	—
	D 26	220	—	10	98	4	—	4	95	9	—	—	—	—
	D 29	342	—	22	221	3	—	4	86	6	—	—	—	—
	D 30	220	—	22	137	6	—	8	43	4	—	—	—	—
	D 33	166	—	7	154	—	—	—	5	—	—	—	—	—
	D 52	244	1	29	163	13	—	—	9	1	28	—	—	—
	D 54	377	2	80	239	6	—	14	27	1	3	3	2	—
	D 56	304	—	40	214	—	—	5	16	—	16	3	9	1
Braunton Burrows	1	56	—	4	4	—	6	18	24	—	—	—	—	—
	2	86	—	7	6	—	7	11	53	2	—	—	—	—
	3	24	—	2	—	—	2	6	14	—	—	—	—	—
	4	21	—	—	1	—	—	10	9	1	—	—	—	—
	5	81	1	10	3	—	—	54	13	—	—	—	—	—
	6	79	4	12	4	—	7	33	19	—	—	—	—	—
	7	25	—	2	—	—	3	10	10	—	—	—	—	—
Crantock		1052	62	357	602	24	1	3	3	—	—	—	—	—
Perranporth		19	12	—	3	3	1	—	—	—	—	—	—	—
Gwithian	1	85	1	2	26	9	1	3	31	12	—	—	—	—
	2	99	30	1	31	2	7	—	24	4	—	—	—	—
N. IRELAND														
Rathlin I.		82	24	8	14	—	19	3	12	2	—	—	—	—
Whitepark Bay	1	101	15	14	23	1	13	15	15	5	—	—	—	—
	2	29	9	2	1	1	4	1	8	3	—	—	—	—
	3	66	11	2	11	7	13	9	8	5	—	—	—	—
	4	23	8	1	5	2	—	1	3	3	—	—	—	—
	5	58	14	2	11	5	4	3	12	7	—	—	—	—
Portstewart	1	22	—	—	4	—	1	—	17	—	—	—	—	—
	2	17	1	—	7	—	—	1	8	—	—	—	—	—
Magilligan Strand		40	—	—	9	—	1	—	30	—	—	—	—	—
Malin Head		52	5	—	17	—	1	—	29	—	—	—	—	—

APPENDIX

TABLE 1 (*cont.*)

locality		total	yellows 0	yellows 3	yellows 5	yellows 5E.U.	pinks 0	pinks 3	pinks 5	pinks 5E.U.	browns 0	browns 3	browns 5	browns 5E.U.
Lough Swilly	1	105	—	1	8	2	1	11	82	—	—	—	—	—
	2	46	—	2	4	—	—	7	32	1	—	—	—	—
Sheephaven		62	—	7	32	—	—	2	21	—	—	—	—	—
Dunfanaghy	1	28	1	—	8	—	—	—	19	—	—	—	—	—
	2	40	2	—	10	—	1	—	27	—	—	—	—	—
N.W. IRELAND														
Tramore Strand	1	102	34	—	62	—	2	—	4	—	—	—	—	—
	2	82	3	3	57	—	—	—	19	—	—	—	—	—
	3	72	—	—	45	—	—	—	27	—	—	—	—	—
	4	26	—	—	19	—	—	—	7	—	—	—	—	—
Ballyness Bay		70	34	—	36	—	—	—	—	—	—	—	—	—
Portnoo		189	18	—	49	1	25	—	78	1	17	—	—	—
near Ballyshannon		76	7	—	17	—	5	—	21	—	19	—	—	7
Bundoran		336	10	—	105	—	6	—	169	—	45	—	1	—
Bunduff	1	107	6	4	51	4	5	3	16	1	17	—	—	—
	2	101	18	14	35	4	18	—	1	1	8	1	1	—
	3	111	6	4	52	17	4	1	8	2	17	—	—	—
	4	138	6	16	56	17	2	1	19	6	15	—	—	—
Clashybawn	1	96	—	5	71	3	—	1	11	1	4	—	—	—
	2	66	1	9	37	4	—	1	2	2	10	—	—	—
Streedagh	1	57	25	1	8	10	4	1	6	1	1	—	—	—
	2	122	50	17	22	6	6	5	10	1	3	—	—	2
	3	262	18	23	56	6	7	22	46	7	6	20	35	16
	4	131	34	33	24	3	35	—	—	1	—	—	—	1
Rosses Point		156	24	17	83	12	1	1	12	4	2	—	—	—
S.W. IRELAND														
Derrynane		286	41	77	106	2	5	27	28	—	—	—	—	—
E. IRELAND														
Corvallis		39	—	1	12	—	1	2	19	—	4	—	—	—
Rosslare Harbour		161	5	3	97	5	6	1	32	—	12	—	—	—
totals		14244	749	1130	5933	239	394	557	4123	143	675	35	227	39
			yellows 8051				pinks 5217				browns 976			

APPENDIX (*cont.*)

TABLE 2. SCORES OF SAMPLES OF *CEPAEA NEMORALIS* FROM THE POINT OF AIR SAND-DUNES

		yellows				pinks				browns	
locality	total	0	3	5	5E.U.	0	3	5	5E.U.	0	3
1	89	—	—	74	—	—	—	15	—	—	—
2	74	—	—	64	—	—	—	10	—	—	—
3	85	—	2	42	—	—	5	36	—	—	—
4	193	—	5	96	—	—	8	84	—	—	—
5	53	—	2	26	—	—	5	20	—	—	—
6	74	—	15	39	—	—	1	19	—	—	—
7	95	—	23	31	—	—	18	23	—	—	—
8	65	—	18	30	—	—	5	12	—	—	—
9	89	—	3	34	1	—	4	44	—	3	—
10	64	—	8	27	—	—	6	18	—	5	—
11	70	—	6	30	—	—	2	26	—	6	—
12	73	—	13	32	—	—	—	5	—	23	—
13	148	1	23	74	1	—	8	31	—	10	—
14	28	—	3	19	—	—	—	1	—	5	—
15	84	—	16	36	—	—	5	15	1	11	—
16	103	—	20	33	—	—	6	20	—	24	—
17	33	—	6	12	—	—	1	4	—	10	—
18	91	—	39	19	—	—	11	9	—	13	—
19	183	—	19	72	—	—	18	59	1	14	—
20	114	—	5	55	—	—	8	44	—	2	—
21	90	—	8	57	1	—	—	24	—	—	—
22	135	—	11	69	1	2	3	41	—	8	—
23	90	—	8	45	1	1	5	26	1	3	—
24	172	3	31	91	2	11	5	27	—	2	—
25	45	—	6	24	—	6	2	4	1	2	—
26	144	—	36	78	—	—	10	17	—	1	2
27	78	1	9	55	—	1	4	7	—	1	—
28	49	4	6	27	—	—	4	8	—	—	—
29	86	1	19	48	—	1	2	15	—	—	—
30	96	—	14	43	—	2	11	25	—	1	—
31	19	—	8	4	—	—	3	4	—	—	—
32	84	—	25	29	—	—	14	16	—	—	—
33	93	—	30	26	—	—	12	14	—	11	—
34	133	—	23	68	—	—	1	8	—	33	—
35	62	—	—	12	—	—	1	48	—	1	—
35*a*	24	—	—	5	—	—	—	19	—	—	—
36	9	—	—	1	—	—	—	8	—	—	—
37	37	—	—	8	—	—	—	25	—	4	—
38	70	—	1	19	—	—	2	44	—	4	—
39	76	—	17	29	—	—	6	3	—	21	—
40	46	1	31	12	—	—	1	1	—	—	—
41	49	—	29	10	—	—	9	1	—	—	—
42	198	1	5	164	—	—	2	26	—	—	—
43	20	—	—	15	—	—	—	5	—	—	—
44	92	—	5	40	—	—	2	44	1	—	—
45	97	—	1	25	—	—	—	71	—	—	—
46	33	—	5	14	—	—	3	11	—	—	—
47	42	—	2	27	—	—	3	10	—	—	—
48	26	—	6	9	—	—	4	7	—	—	—
49	22	—	—	14	—	—	—	8	—	—	—
50	958	—	128	407	—	—	83	340	—	—	—
A	45	—	31	12	—	—	—	2	—	—	—
B	32	—	20	8	—	—	1	3	—	—	—
C	15	—	8	5	—	—	—	2	—	—	—
D	9	—	4	1	—	—	1	3	—	—	—
E	10	—	—	2	—	—	—	8	—	—	—
	5094	12	753	2348	7	24	305	1420	5	218	2
	totals	yellows 3120				pinks 1754				browns 220	