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POLYMORPHISM IN CEPAEA NEMORALIS (L)

by

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POLYMORPHISM IN CEPAEA NEMORALIS (L)

Introduction

The snail *Cepaea nemoralis* is one of the classic organisms in the study of polymorphism in natural populations. Relatively little seems to be known about other polymorphic land snails and it was originally intended that the work for this dissertation would be on one of these less-studied species. Two species that might have proved suitable are *Helicella virgata* and *Hygromia striolata.* Unfortunately *H. virgata,* a highly polymorphic species matures during late summer and dies in the winter, and so was not available at the right time. *H. striolata*, a dimorphic species, although available in the adult stage during May, June and July appears to be scarce in Durham; in fact two weeks of searching did not yield one specimen.

During the period spent looking for *H. striolata* an old magnesium limestone quarry (Wingate quarry) was found where *cepaea nemoralis* were abundant and thrush predation of this species appeared relatively heavy. The following is based on the work done on *C. nemoralis* at this quarry and at other suitable sites on the magnesium limestone, east of Durham City. The abundance at Wingate quarry was not indicative of the abundance in Durham in general; considerable searching was necessary before the sites described below were found. For some reason *C. nemoralis* is not successful in the more industrialised areas (Taylor 1914). All the sites are areas of scrub grassland except one, an area of reed grass at Wingate quarry, as *Cepaea* was rarely found in other types of habitat (one snail was found in the numerous areas of woodland searched). However, the reasonable uniformity of the habitats provides a useful basis for comparison.

Despite all the work done on *C. nemoralis*, the factors that maintain the striking polymorphism in this species are only partially understood, and it is becoming increasingly apparent that different factors are important in different places. Opinions on the subject tend to be polarised with respect to the importance of selection and the importance of drift (Cain and Currey, 1963, Goodhart 1963).

Systematics and Distribution

The genus Cepaea (Held 1837) contains four closely related species. *C. vindobenensis* is confined to south-eastern Europe and the Caucasus, and *C. sylvatica* to the Western Alps. *C. hortensis* is found in north, central and western Europe, from Finland to the Pyrenees and the British Isles, and as far as Iceland and north-eastern North America. *C. nemoralis* is confined to central and western Europe from Northern Italy, and Czechoslovakia, to the Pyrenees, Ireland, South Scotland and Southern Scandinavia. *C. sylvestica* and *vindobenensis* both have a haploid chromosome number n=25; *C. hortensis* and *nemoralis* have n=22 (Periot and Periot 1938). Hyrbridization between *C. hortensis* and *C. nemoralis* can occur, but it is extremely rare in the wild (Lamotte 1951).

Genetics

A good deal of work has been done on the genetics of *C. nemoralis* (Cain and Sheppard 1957, Cain, King and Sheppard 1960). The three principal colour morphs are brown, pink and yellow, which are respectively due to violet, pink and yellow pigments, in the calcareous layers of the shell, showing through a thin brownish-yellow periostracum. Yellow and pink are allelomorphic, pink being dominant to yellow, and brown, which is dominant to both pink and yellow, is either allelomorphic or at a different but closely linked locus. Five separate dark brown bands superimposed on the ground colour is the basic banding pattern and this is recessive to the allelomorphic unbanded condition. The locus for banding is closely linked to that for colour. A single middle band (formula 00300 - the bands are numbered 1 to 5 from top to bottom of the body whorl, 0 indicating absence of a band) is dominant to the five banded condition but recessive to the unbanded, and is at a different locus. The inheritance of other patterns in which bands are missing has not yet been worked out. The various degrees of band fusion appear to be multifactorially controlled, and the common variety *punctata* (moq) in which the pigmentation of the bands is unevenly distributed, giving them a dotted appearance, is dominant to the normal continuous dark banded condition. Dominance is incomplete in some heterozygotes for instance in pale pink/yellow heterozygotes.

Polymorphism

Polymorphism (or morphism, Huxley 1955) has been defined by Ford (1945a) as the condition existing when genetic variants or morphs co-exist in temporary or permanent balance within a single interbreeding population in such frequencies that the rarer cannot be maintained solely by mutation or by the spread of selectively neutral mutants.

Nearly every colony of Cepaea that has been looked at has shown polymorphism; out of 800 studied by Lamotte only two were monomorphic. There is fossil evidence to show that the morph frequencies in certain areas have remained approximately constant since Neolithic times (Diver, 1929), and Goodhart (1954) has shown that two populations he studied in France have remained remarkably constant for 40-50 years. Although it has been claimed that mutation maintains the polymorphism in C. nemoralis (Lamotte 1951) it is generally thought that this is most unlikely as the mutation rate would have to be exceptionally high.

Before the work of Cain and Sheppard (1950), the polymorphism in Cepaea was generally quoted as being an example of drift. Diver (1940) could find no other explanation than that of random processes and considered that the patterns had no selective value, and on the basis of his evidence similar conclusions have been reached by a number of authors (Dobzhansky 1941, Huxley 1942, Mayr 1942).

In 1905 Dr. Dale (quoted by Taylor) suggested that the striped shell of C. nemoralis might conceal it from predators. The work of Cain and Sheppard (1950, 1952, 1954, Sheppard 1951) has shown quite conclusively the importance of camouflage from predators as a factor determining the population structure of C. nemoralis in the areas they looked at 'round Oxford. They collected shells from six types of habitat, ranging from beechwoods to scrub grassland and showed that the frequency of banding was less on uniform backgrounds (e.g. a "carpet" of beech leaves) than on broken backgrounds (scrub grassland) and that shell colour was correlated with the colour of the background, pink being more common on dead leaves, and yellow (slightly greenish with the animal inside the shell) more common in grassland. Sheppard (1951a) found that in a wood near Oxford thrushes predate the more conspicuous morphs, and that a morph inconspicuous in early spring (on dead vegetation) became more conspicuous, and was predated more heavily, as the background changed. Goodhart (1958) has shown that a similar pattern occurs in a *C. hortensis* population near Cambridge.

Clarke (1962) has suggested that *C. nemoralis* morphs may be predated not because of their conspicuousness, but because of their frequency; very common morphs although they may be less conspicuous than others, would be predated more if predators formed a searching image of shells they encountered most ~~green~~ often. There is good evidence that thrushes can form searching images (Clarke 1962), but evidence to show that frequency dependent selection operates in *cepaea* populations is scanty and inconclusive. (The type of frequency dependent selection in which rare phenotypes are at an advantage is sometimes called apostatic selection).

The predation theories do not explain all the characteristics of *C. nemoralis* populations that have been observed, otherfactors appear to be involved. As Lamotte (1959) and Goodhart (1962, 1963) have pointed out there is considerable variation between *cepaea* populations from apparently similar habitats. Conversely, Cain and Currey (1963) have described populations of *Cepaea* from Marlborough Downs which keep the same composition over a wide area in which there are a variety of habitats (the area effect). These characteristics have been variously attributed to climate factors and random processes. The importance of the relation between climatic factors and *Cepaea* polymorphism has been stressed by a number of authors (Lamotte 1959, Arnold 1969). Arnold's work in the Pyrenees has shown that yellow unbanded shells are favoured in drier hillside habitats and banded in damper riverside habitats. Lamotte carried out experiments in which *Cepaea* were heated for 40 minutes under a 150 watt bulb and found that mortality rose in the series 00000-00300-12345 and that yellow survive better than pink. A point generally agreed upon is that internal genotypic selection is an important, perhaps the most important, factor in the maintenance of polymorphism in *Cepaea* (Ford 1964).

METHODS

Collecting

C. nemoralis is usually only active during the crepuscular and nocturnal hours, but it will emerge during the day after rain. Because much of May, June and July was very dry this year, many of the samples were collected early on dewy mornings and only a few during the day. To avoid bias in collecting, due to differences in the conspicuousness of the various morphs, an area in each site sampled was searched very thoroughly, often on hands and knees. The number of snails collected depended largely on their abundance, which varied considerably among the sites, but a minimum of 50 shells was collected when possible, and an effort was made to collect enough to include at least five specimens of the rarest type, although this was not always achieved.

Scoring the Shells

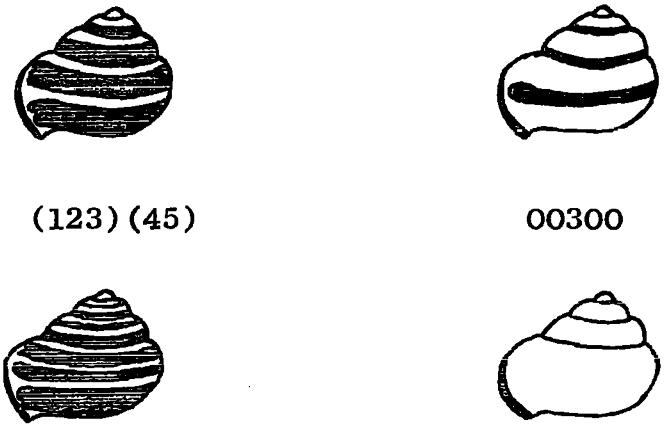
In all samples except those from Wingate quarry which were replaced for the purpose of the predation observations, the snails were removed from their shells before scoring by placing them in hot water for about five minutes and then extracting them with a needle.

Only pink and yellow shells were found. Because of the considerable variation within the pink class its division into two classes, light and dark pink, was considered, but because the range of colour was continuous between light and dark, and a majority of shells were intermediate and difficult to place, only one class was used. Only live shells were included in the sample; predated shells were collected separately.

For scoring the shells according to banding pattern, the system used was that of Von Martens (1832) as modified by Cain and Sheppard (1950). The bands on the body whorl are numbered 1 to 5, the uppermost being 1. A five-banded shell is represented by 12345, and one with the first two bands missing by 00345. Band fusions are indicated by bracketting the corresponding numbers together (see Fig. 1 which shows some of the commoner banding patterns). Because band fusion may begin at any time during growth, bands were considered fused if they were fused at and after a line drawn across the body whorl from the umbilicus at right angles to the lower lip of the shell mouth.

12345

Ventral side of a shell,
with the umbilicus in the centre



(123)(45)

00300

(12)3(45)

00000

FIG. 1. Common Banding Patterns in <u>C. nemoralis</u>. The dotted lines in the top two diagrams indicate the position at and beyond which bands must be fused to be classified as such.

PLATE 1

Wingate Site 5

Wingate Site 1

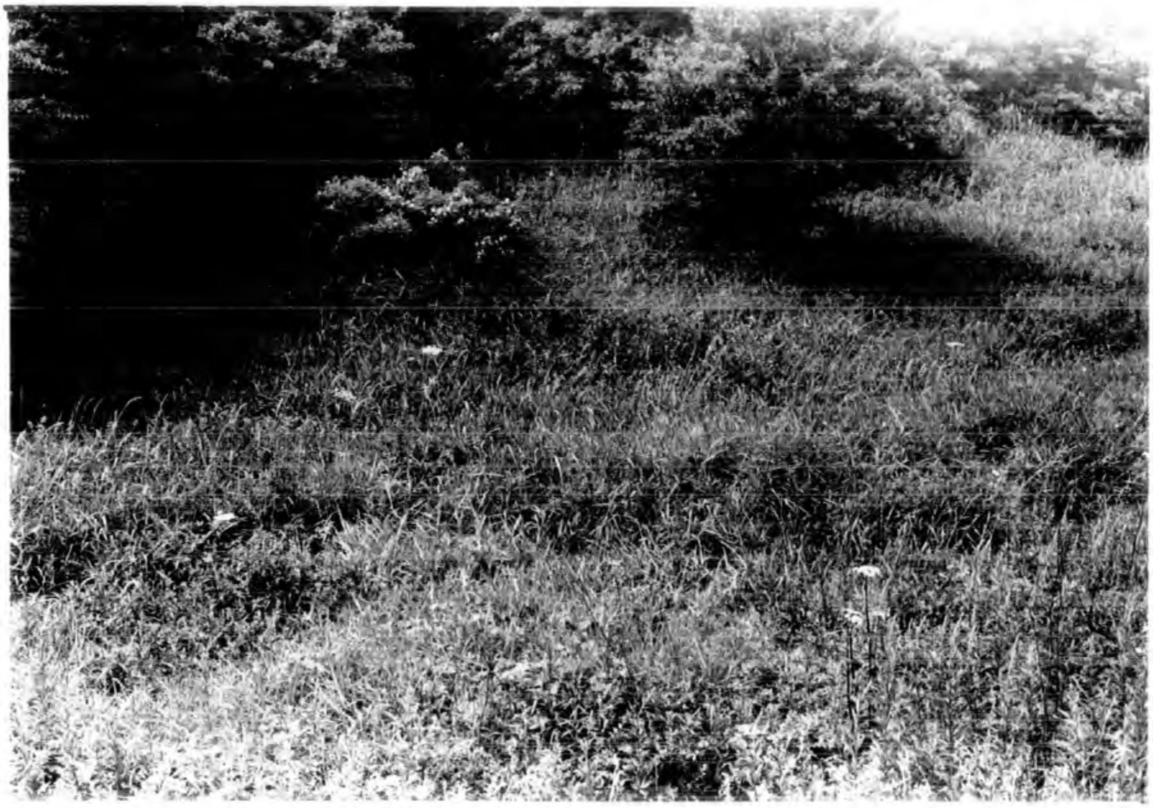


PLATE 2

Wingate Site 6 (at top of quarry face)

Railway cutting running south from Trimdon Station

THE QUARRY SAMPLES

The sites sampled are shown on the map of East Durham in the Appendix (Page 50). All except one of the samples came from areas of scrub grassland in or near quarries, often small areas situated between fields and a quarry face. (A typical site is shown on plate 2). The vegetation in all sites was very similar, and the plant species found at each site are listed in the Appendix (page 48-49). The Bishop Middleham, Wingate, Trimdon and Coxhoe 2 quarries are now disused, but the quarry on the B1283 (the B1283 quarry) between Haswell Plough and Easington, and the Coxhoe 1 quarry are still in use. The samples of *C. nemoralis* collected are classified in tables 1, 2 and 3 in the Appendix.

In Wingate quarry *C. nemoralis* was fairly abundant and seven samples were collected in all. In all the other quarries only one sample was taken, as in the time available after the sampling at Wingate was complete, an attempt was made to find and sample as many places as possible in order to get some idea of the extent to which populations of *C. nemoralis* varied. Thus the quarry work discussed in this section can be divided in to two parts; the more detailed study of *C. nemoralis* in Wingate quarry; and the more general study of the other six quarries, and their comparison with Wingate.

Wingate Quarry

On page 51 in the Appendix is a pull-out map of the part of Wingate quarry sampled. Five samples were taken along a transect in the more central part of the area shown, and the other two were taken from sites over 200 metres away on either side of this area (one of these sites, site 6, is shown on plate 2). Site 1 is an area of scrub grassland surrounded on two sides by dense patches of hawthorn bushes, on the third by a quarry face (which drops away vertically from the level of the grassland) and on the fourth by a path 2 metres wide (plate 1). Beyond the path is a bank which forms one side of a large quarry tip now well covered by scrub grassland; part of this is site 2. Site 3 is an area on top of the tip and site 4 is on the west-facing bank of the tip. Site 4 is separated by a path 3 metres wide from another bank which descends to site 5, an area of reed grass, meadow sweet and nettles, partially surrounded by large hawthorn bushes, close to a stream. The distances between each area sampled are shown on the map. The purpose of this sampling procedure was to discover the extent to which morph ratios varied over a short distance and the response, if any, to the different conditions of an exposed bank, a more sheltered area of scrub grassland (site 1) and an area of reed grass. Sites 6 and 7, which were areas higher up at the top of quarry faces, were sampled to get a general picture of the variation throughout the quarry.

Over the entire quarry there was a good deal of variation in the proportions of the different morphs; for sites 1-5 this is expressed graphically, in Fig. 1. Pink band, yellow banded, and pink and yellow unbanded snails were the predominant types found; the only other type being one with a white instead of a black peristome lip but these were so infrequent that they were not recorded separately but grouped with the main classes. The frequency of pink banded snails varied from 21% to 46%, yellow banded from 15% to 34%, pink unbanded from 6% to 30% and yellow unbanded from 13% to 40%.

Each sample was compared with every other using a 4x2 Chi-squared test (the values of Chi-squared are shown in Table 9 in the Appendix). Samples 6 and 7 were significantly different from each other and from every other sample ($P<.01$) . A pattern in the variation along the transect from site 1 to site 5 can be seen; sample 1 is insignificantly different from samples 2 and 3, and sample 2 is insignificantly different from sample 3, but samples 1, 2 and 3 are significantly different from 4 and 5 ($P<.05$) which are insignificantly different from each other.

A similar pattern is shown by the variation in banding patterns between the samples (Table 3). The banded shells from each sample have been divided into two categories, those showing fusions between one or more bands and those with no fusions. Each sample was compared with every other sample using a 2x2 Chi-squared test. Samples 6 and 7 were significantly different from all other samples ($P<.05$) except sample 1. Sample 1 was not significantly different from sample 2 but was from samples 3, 4 and 5 ($P<.05$) and samples 4 and 5 were not significantly different, but differed from sample 3.

All that could be found out about the history of Wingate quarry is that it was abandoned in the 1920's.

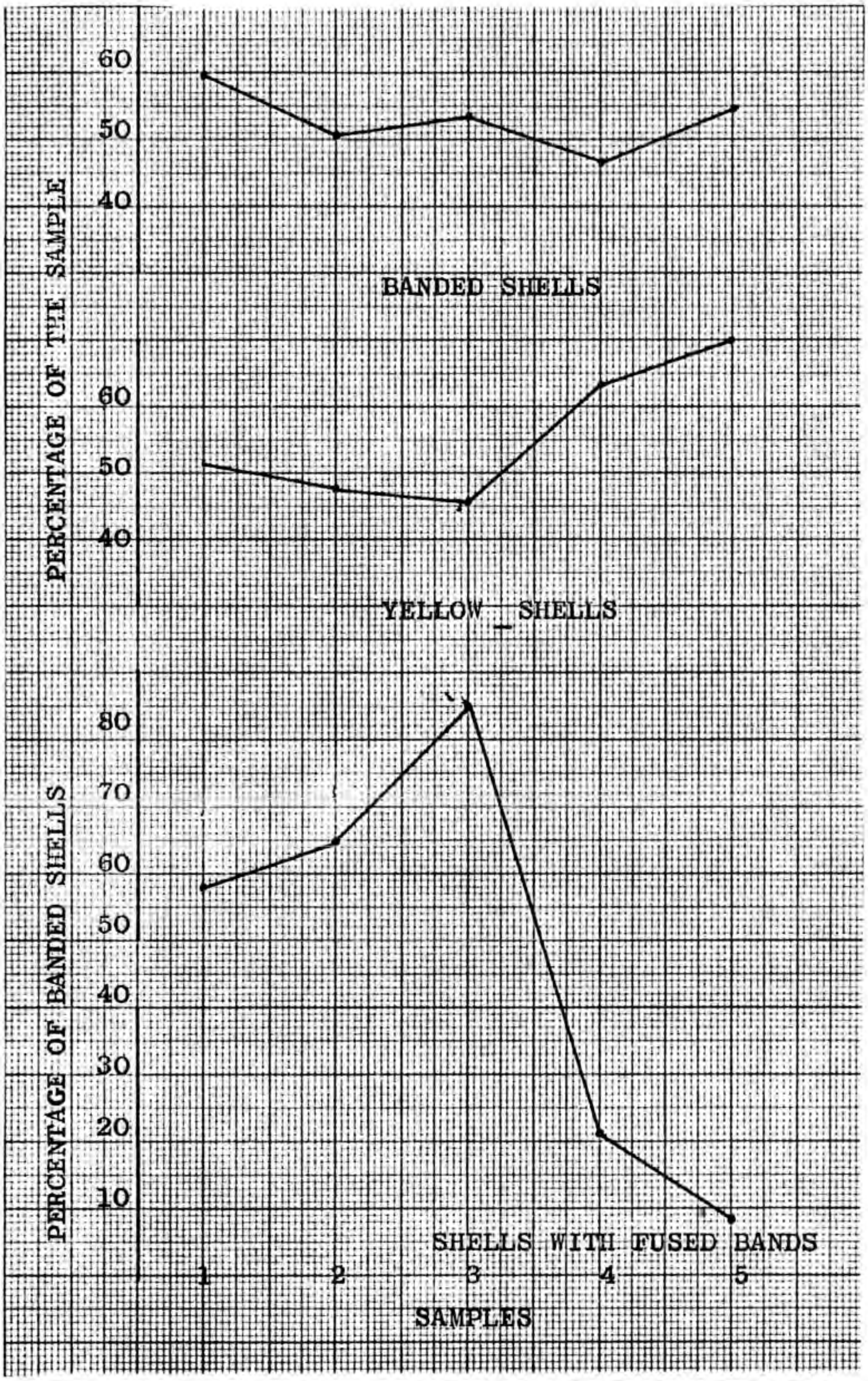


FIG. 2. VARIATION BETWEEN WINGATE SAMPLES 1-5.

The pattern of variation between samples 1 to 5 suggests that the quarry waste tip, once overgrown by vegetation, was colonised by snails coming from areas on either side of it. Sites 1 and 5 are both partially surrounded by large hawthorn bushes and appear to have been in existence for some time (the grassland of site 1 could have been maintained by gazing, although this no longer occurs). On the tip, apart from the scrub grassland, there are only a few small hawthorn bushes and patches of brambles, and it appears to be of more recent origin than sites 1 and 5 (in places there are still areas of bare stones). It seems reasonable to postulate that the waste tip has been colonised by Cepaea, probably within the last 15 years from two different populations (perhaps part of a continuous population before the tip was first formed) situated on either side of it and coming from different habitats. Up till now the snails on either bank have maintained the identity of the population from which they originated despite the similarity between the banks, and the marked difference between the site 4 and site 5. If this hypothesis is well-founded it would be interesting to see for how long the snails on the two banks maintain their differences, and how they change, when and if they do.

The samples from sites 6 and 7 are similar to sample 1 in banding pattern, and it is worth noting that out of the 7 samples only these three come from scrub grassland based on a natural limestone formation. But in other respects the differences between these samples are very significant.

The Other Quarries

The only other quarry sample besides those from Wingate that contained unbanded snails came from the Bishop Middleham quarry, which lies about 10 miles to the south east of Durham City just off the A177. The Bishop Middleham site was most similar in appearance to site 1 of Wingate; it was partially surrounded by large hawthorn bushes, under which were anvils, and bordered on one side by a quarry face. A Chi-squared test showed that the samples from these two sites were not significantly different. The plant species found at the two sites were similar and are listed in the Appendix on page 48-49.

In all the other quarries sampled, no unbanded snails were found (except for a single yellow unbanded juvenile at Coxhoe 2). The normal dark banded pink and yellow snails were the most common morphs, but the dotted banded variety (punctata) was occasionally found. The frequency of pink banded snails among the five samples varied between 27.9% and 52.5% and of yellow banded between 26.9% and 69% (see Table 2). The sites at Coxhoe 1, Coxhoe 2 and the Garage quarry were exposed areas of scrub grassland at the top of quarry faces, the Trimdon site was a bank of a quarry waste tip and the B1283 site was an area of scrub grassland dotted with hawthorn bushes, a short distance from ~~the~~ a quarry.

Each of the five samples was compared with every other by means of a 2x2 Chi-squared test; dotted banded snails were grouped with the normal dark banded type. There were significant differences between most of the samples, only the following were not significantly different - those from Coxhoe 1 and the Garage quarry, from Coxhoe 2 and the B1283 quarry, and from Trimdon quarry and the Garage quarry. Apart from the similarity between the Coxhoe 1 and the Garage quarry sites, the results were not what might be expected on the basis of the visual similarities between the sites, although this criterion might be misleading. (The similarity between the Coxhoe 2 and B1283 samples is only partial as the latter contained snails with dotted bands).

To examine differences in the frequency of the various banding patterns among the samples, each one was divided up into the following categories: 12345, (123)(45), (12)3(45), others with band fusions, and 00300. Instead of comparing samples individually, they were grouped together and tested for heterogeneity using a 5x5 Chi-squared test. The heterogeneity among the samples was very significant ($P \leq .001$).

The difference between the Wingate samples and the five described above is obvious, but cannot be demonstrated statistically due to the absence of unbanded snails in the latter. If differences in habitat are the cause of this variation they are far from obvious. Two more similar looking habitats than site 6 at Wingate and the Garage quarry site would be hard to find; both are areas of typical limestone scrub grassland, bordered on one side by a quarry face which drops vertically down, and on the other by fields, from which they are fenced off. Yet the sample of Cepaea nemoralis from site 6 at Wingate was 65% unbanded, and that from the Garage quarry 100% banded. No predated shells were found at either site.

PREDATION

The work of Cain and Sheppard (1950, 1952, 1954, Sheppard 1951) and Goodhart (1958) has shown that the proportions of the different morphs in colonies of Cepaea near Oxford and Cambridge are affected by selective visual predation. The main predator of Cepaea in many areas is the song Thrush (Turdus ericetorum) which feeds on snails when earthworms and fruit, its chief food, are not available.

The study of thrush predation on Cepaea is greatly facilitated by the thrush anvil, a stone, or any other hard surface, used by the thrush for breaking shells. The shells are left surrounding the anvil and can easily be collected for analysis. The snail-eating behaviour of thrushes has been described by Morris (1954a). The thrush hunts systematically through a patch of vegetation and when a snail is found it carries it to an anvil breaks and eats it, returns to the area through which it was working and resumes the search. The distance between the anvil and the place of capture is usually short; a thrush will make use of the nearest suitable anvil.

Various rodents are known to predate snails, but their importance is uncertain. Cain and Sheppard (1954) suggested that rabbits predating snails according to their visual tone might have been responsible for the banding patterns in some of their samples, and Goodhart (1962) found evidence of rat predation along the Hundred Foot Bank near Cambridge. Small field rodents and squirrels have also been known to take snails. Thrush and rodent predated snails can be distinguished by the areas of the shell broken; a thrush holds the snail by the lip and cracks parts of the shell away from the lip, but rodents bite into the shell and the area removed often includes some of the lip.

The collections of predated shells described below all came from around a stone, or from some other hard surface that could have been used as an anvil and were nearly all broken in areas away from the lip. No predated shells were found in the grass from which samples were taken.

Predation at Wingate Quarry

Site 1 at Wingate quarry, described above, is particularly suitable for studying thrush predation of Cepaea. The snails are fairly abundant in the grass, and under the surrounding large hawthorn bushes are a number of thrush anvils that have been well used in the past. The anvils from which shells were collected were all near the edge of hawthorn bushes nearest site 1, which was almost certainly the area predated.

In an attempt to confirm that the area predated was site 1 the snails collected from here were marked by piercing the shells with a small hole near the edge of the lip on the underside of the shell towards the umbilicus, and replaced. (Only adult snails were marked). The nearest alternative site to site 1 was site 2, and snails sampled from this area were marked with two holes in case thrushes carried shells from here to the cleared anvils surrounding site 1. (If any of these shells had been found round the anvils, the possibility that the snails had migrated from site 2 to site 1 would have needed consideration).

Site 5, the area of reed grass, nettles and meadowsweet by a stream was also partially surrounded by large hawthorn bushes under which there were thrush anvils. Old predated shells were nothing like as abundant here as at site 1 but enough were collected for the purpose of analysis. As for site 1, the snails collected were marked and replaced, but unfortunately only 3 newly predated shells were found round the cleared anvils during the period of study, perhaps due to the height and density of the vegetation at this time; thrushes may find snails more easily here later on in the year when the vegetation has died down, or earlier in the year when growth is beginning.

Old predated shells were collected, and the anvils cleared, in May, and the anvils were revisited at 20-day intervals. Each so-called anvil was an area of 1-2 square metres covered by dead hawthorn twigs and scattered stones. Apart from sites 1 and 5, old predated shells were collected only from an anvil at site 3; there were very few found along the paths bordering sites 2 and 4, and none found at sites 6 and 7, perhaps due to the lack of suitable anvil sites.

Monthly Variation in the Predation Rate

This was similar to that described elsewhere (Goodhart 1958, Davis and Snow 1965, Cameron 1969) in that a very clearly defined peak was reached (see Fig. 2 opposite). During May very few predated shells were found, in June the number increased, in July there was a peak, and in August a decline (in August shells were collected after only 10 days). Davis and Snow found that the main food of the thrush became scarce during the late summer and thought this the reason for the increased predation on snails. Goodhart has suggested that the increase is correlated with the flying of the last brood, although thrushes have been seen feeding young, still in the nest, on snails (Morris 1954a).

Use of the Anvils

Out of the 123 new shells collected from the four cleared anvils surrounding site 1, 80 came from one anvil (anvil 1). Anvils 3 and 4 may not have been used so much because they became partially overgrown with nettles and other herbs during June and July. Anvil 2, like anvil 1, remained clear of vegetation but yielded only 8 shells, although numerous old predated shells had previously been found there. According to Morris a thrush is likely to return to the same anvil each time it returns to a snail population not because it remembers it but because it is convenient and will be happened on afresh each time. The evidence he bases this conclusion on comes from his observations in a garden with a large area of concrete paths which were used as anvils, and he suggests that it might be to the thrushes' advantage to memorise the location of anvils in areas where they are scarce. Anvils were not particularly scarce around site 1, although far less extensive than the above-mentioned concrete paths, but on the other hand they were concealed by hawthorn bushes and could not be seen from outside. A thrush searching the area of grassland adjacent to anvils 1 and 2 (they were only a couple of metres apart), if it searched randomly for anvils once a snail was found, would be expected to use anvils 1 and 2 equally if there was no difference between them. The fact that anvil 1 was used so much more than anvil 2 suggests that either there was an unseen difference or that the thrush was memorizing the position of anvil 1.

Marked Shells

6 out of the 109 shells originally marked were found predated, all at anvil 1. Considering that the original sample was taken from only part of the grassland near the anvils and once replaced would have become mixed with unmarked shells, and also that the thrush must sometimes have looked for snails in parts of site 1 not sampled, the 6 shells give a good indication that the area predated is near the anvils.

Comparison of the Predated Shells and the Snail Population

The predated shells are classified in Tables 5, 6 and 7 ~~and~~ in the Appendix. In the following analysis all the newly predated shells from site 1 have been lumped together; ~~and~~ the percentage of the different morphs among them, and of the morphs in the sample taken from site 1, are shown below:

	Pink Banded	Yellow Banded	Pink Unbanded	Yellow Unbanded
Newly predated shells	43.9	25.2	11.4	19.5
Site 1 sample	34.4	25.5	14.0	26.2

According to Cain and Sheppard, banded shells should be less conspicuous than unbanded shells against the broken background provided by scrub grassland, and so should suffer proportionately less from predation (assuming that what is conspicuous to man is conspicuous to a thrush). The above results show the opposite to this, unbanded shells have been predated proportionately less than the banded, and among the banded shells the pink banded, but not the yellow banded, have been predated proportionately more. Comparison of the predated shells and the site 1 sample by means of a 4x2 Chi-squared test show them to be insignificantly different, $P > .05$ (values of Chi-squared are shown in the Appendix in Tables 8 and 9) but the differences shown in the above table are worth noting as they are corroborated by the comparison of the old predated shells with the site 1 sample, discussed further on.

To group all the banded shells together, as done above, might be misleading. The idea that banded shells should be less conspicuous in a broken habitat is based on the fact that bands break up the outline of the shells. In general, the most important bands as far as camouflage is concerned are the uppermost (bands 1, 2 and 3) for these, especially 1 and 2, will be seen by a thrush looking down on the shell while bands 4 and 5 will be hidden from view. If the uppermost bands are partially or completely fused a block of colour is presented to the thrush and the camouflaging function of the bands will be partially negated. To examine the relation between fusions and predation the predated shells and the site 1 sample (adult snails only as band fusion often developes late) were divided into the following three categories: effectively banded shells (bands 1, 2 and 3 separate); intermediate shells (bands 1, 2 and 3 completely or partially fused) and effectively unbanded shells (including shells with the first two bands missing). The few shells with a single band missing, and with no fusions, were included in the former class. The Table below shows the newly predated shells and the site 1 sample classified in this way. Numbers are expressed as percentages:

	Effectively banded	Intermediate	Effectively unbanded
Site 1 predated shells	45.1	24.1	30.8
Site 1 sample	48.6	15.6	35.8

A comparison of the predated shells and the sample, classified as above, using a 3x2 Chi-squared test, again shows no significant difference ($P > .05$). But it should be noted that the greatest difference shown in the above Table is between the intermediate classes, and the trend is as predicted.

Old Predated Shells

The morph frequencies, expressed as percentages, among the old predated shells from Wingate quarry, and in the samples from the relevant sites are shown in the Table below:

	Pink banded	Yellow banded	Pink unbanded	Yellow unbanded
Site 1. Old predated shells.	43.7	21.6	16.1	18.4
Site 1 sample	34.2	25.7	14.0	26.1
Site 3. Old predated shells.	37.5	18.0	15.3	29.2
Site 3 sample	35.3	18.5	18.8	27.4
Site 5. Old predated shells.	27.3	31.2	9.1	32.4
Site 5 sample	20.9	36.5	8.5	36.5

Comparison of the predated shells and sample from site 1 using Chi-squared, shows that the two are very significantly different (P = .01). As the composition of the newly predated shells suggested, banded shells are predated relatively more than unbanded shells, and among the banded shells the pink banded, but not the yellow banded, are the ones subject to excess predation.

For sites 3 and 5, Chi-squared tests show predated shells and respective samples to be insigificantly different, but again the results are consistent insofar as banded shells occur relatively more frequently among the predated shells.

The old predated shells and respective samples are classified as effectively banded or intermediate or effectively unbanded in the Table below:

	Effectively banded	Inter-mediate	Effectively unbanded
Site 1 predated shells	41.4	23.9	34.6
Site 1 sample	48.6	15.6	35.8
Site 3 predated shells	19.6	35.7	44.5
Site 3 sample	19.7	33.7	46.5
Site 5 predated shells	47.4	11.0	41.6
Site 5 sample	52.4	3.6	44.0

The above figures indicate that the shells with fusions among the top three bands are predated relatively more than the other two classes and although Chi-squared tests show no significant difference between predated shells and samples

(P>.05) the consistency is interesting.

The above results for new and old predated shells show good agreement despite the lack of statistical significance. There is a reasonable indication that banded shells as a whole are predated relatively more than unbanded and that pink banded shells are predated relatively more than the other morph types. Banded shells with fusions in the first 3 bands appear to be predated relatively more than effectively banded and effectively unbanded shells.

These differences could be explained in one of three ways. Firstly, the old predated shells might have been predated when the snail population had a different composition than it has now, and the similarity between them and the newly predated shells, which are not significantly different from the population, might be due to chance. Secondly, banded shells with fusions among the first three bands, might be more conspicuous than other types of shell to the thrushes at Wingate quarry. Thirdly, thrushes may form predation images of the more common morphs in the population and predate proportionately more of them, less frequent morphs being overlooked even if they are more conspicuous. Little can be said about the first alternative; whether the population is stable or not is not known. Some of the old shells could have been predated between five and 10 years ago (Goodhart 1962).

Unless fusions in the uppermost bands are in some way associated with the pink locus, the fact that relatively few yellow banded shells appear among the predated shells makes the second explanation less likely. As far as the numbers available permit analysis of this point they show the reverse if anything; fusion in the uppermost bands among all predated shells from site 1 are more frequent among yellow shells than pink, but the difference is not significant. In the sample from site 1 the difference is the same but highly significant (P = .001). So for site 1 yellow shells appear to have a relatively greater degree of fusion in the uppermost bands. In the sample from site 3 fusions are significantly more frequent among yellow shells (P = .05) but among the predated shells there is a slightly higher proportion among the pink, but the difference is insignificant.

Although the results are inconclusive, they do show that frequency dependent predation, affecting pink banded shells, could be occurring.

Predation in other Quarries

In four of the other quarries sampled besides Wingate (Coxhoe 1, Coxhoe 2, Trimdon and Bishop Middleham), enough predated shells were found to permit analysis. All the shells appeared to have been predated by thrushes. In the following Table the percentages of the morph types found among the predated shells and in the relevant sample are shown.

Site	Pink banded	Yellow banded	Pink unbanded	Yellow unbanded
Bishop M'ham				
Sample	42.6	15.8	18.3	23.2
Predated shells	43.3	16.1	21.9	18.7
Coxhoe 1				
Sample	37.0	63.0		
Predated shells	35.8	64.2		
Coxhoe 2				
Sample	53.2	46.8		
Predated shells	39.0	61.0		
Trimdon				
Sample	28.5	71.5		
Predated shells	21.0	79.0		

In no case were the sample and predated shells significantly different from each other with respect to the morph types listed above. The Bishop Middleham sample and predated shells were remarkably alike in composition and so were the Coxhoe 1 sample and predated shells. Only 18 predated shells were collected at Coxhoe 2 and the high proportion of yellow banded and the low proportion of pink banded morphs among the predated shells may be due to sampling error. The Trimdon results show a similar, but smaller difference (based on 43 predated shells).

The predated shells and samples from the four quarries are classified according to their postulated conspicuousness to predators in the Table below (numbers in per cent).

Site	Effectively banded	Intermediate	Effectively unbanded
Bishop Middleham			
Sample	36.6	19.5	43.6
Predated shells	40.8	19.7	40.5
Coxhoe 1			
Sample	15.7	70.8	13.5
Predated shells	10.9	84.0	5.1
Coxhoe 2			
Sample	24.5	40.0	36.0
Predated shells	27.8	33.3	38.9
Trimdon			
Sample	46.8	27.9	25.3
Predated shells	46.5	20.9	32.6

Except for Bishop Middleham, the effectively unbanded class consists almost entirely of single banded shells (00300). The Bishop Middleham sample and predated shells are again remarkably similar. The Coxhoe 2 and Trimdo results show the same differences which, as before, are contrary to the Wingate quarry results, the intermediate class being less frequent among the predated shells in both cases. Only the Coxhoe 1 sample and predated shells are significantly different (P=.01). (The comparison was made between 86 snails and 119 predated shells). As in the Wingate results there is a marked excess of shells of the intermediate type among the predated shells, and fewer effectively banded and effectively unbanded shells, than in the sample. This again suggests that a block of dark colour on top of the shell is more conspicuous to predators than anything else.

(N.B; Throughout this section percentages rather than actual numbers are shown in the Tables. When apparently similar differences are in one case statistically significant and in another not so, this is because the actual numbers involved are different. These are shown in the Tables at the back).

COMPARISON OF YOUNG AND ADULTS

C. nemoralis stops growing when it becomes sexually mature and forms a black peristome lip; this provides a definite distinction between the young and adults. The rate of growth of an immature snail is variable depending on temperature, rainfall and food supply. Usually maturity is reached after two years, but occasionally when conditions are favourable a snail hatched at the beginning of one season may be able to form its black lip before the autumn of the following year. Snails are long-lived for invertebrates, and a C. nemoralis can probably survive for 10 years if it escapes enemies (Goodhart 1962).

If some external factor is affecting the frequencies of the different morphs in a C. nemoralis population and this factor remains constant over a number of years, then each age group should change with time in an approximately similar way. For instance , constant predation of a particular morph should make that morph less frequent in older age groups.

In the Wingate samples, and some of the others, young snails were abundant enough for comparisons to be made between them and the adult snails. Because very small snails are difficult to see and will sometimes be missed even in a thorough search, bias in favour of more conspicuous morphs is more likely to be introduced if these are collected. To avoid this, only shells of approximately one third or more of the adult size were collected.

The large range of size among immature snails prompted an attempt to divide them into younger and older categories to illuminate trends. The size of the shell provided a simple method of classification and all young shells were grouped into those with 4 or 3 whorls and those with 5 whorls. But there are two deficiencies in this method as far as analysis is concerned; firstly, the younger group was biased towards the older group because small snails were not collected and the large 4-whorled snails (the majority of the younger age group) and the small 5-whorled snails probably differed in age by only a few weeks. Secondly, division of the young into two age groups increased the likelihood of sampling error. Therefore, for the purposes of analysis all the young have been grouped into one category. (See Table 10 in Appendix).

For the Wingate samples the young and adult snails were compared using a 4x2 Chi-squared test. For the other samples, in which there were no unbanded shells, a 2x2 Chi-squared test was used. In no case was there a significant difference between young and adult snails. (For values of Chi-squared see Table 11 in the Appendix).

In Table 10 (Appendix) frequencies of the various morphs are expressed as percentages of the young and adult samples for purposes of comparison. In view of the conclusions drawn from the predation data the trends indicated are contrary to expectation. In the Wingate samples banded shells are more frequent among the adults than among the young in all except samples 3 and 4. The same is true for pink banded shells in all samples except 4 and 6.

Goodhart (1962) found that among C. nemoralis sampled from the One Hundred Foot Bank near Cambridge about 10% more of the older snails were effectively banded compared with the immature ones. (This was so whatever the proportionate frequency of the banded shells ~~on~~ in the sample). He suggested that this might be due to differential predation or to differential survival due to some other cause, perhaps physiological in origin. The above results suggest that morphs other than pink banded suffer more from such undefined causes than do pink banded. However, it is possible that bias in favour of the more conspicuous unbanded morphs among smaller snails could have come about due to errors in sampling.

The results for Coxhoe 1, Coxhoe 2, Trimdon and the Garage quarry, show no consistent trends. At Coxhoe 2 and Trimdon pink banded are relatively more frequent among the young, and at Coxhoe 1 and the Garage Quarry they are less frequent.

As there ~~is~~ are no significant statistical differences between young and old, the differences shown by the percentage analyses are of questionable validity.

SAMPLES FROM RAILWAY CUTTINGS

A way to assess the relative importance of selection and random processes in the determination of morph frequencies in populations of a polymorphic species is to compare samples from very similar habitats. Goodhart (1962) sampled C. nemoralis at furlong intervals for two miles along the Hundred Foot Bank near Cambridge and found considerable variation among the samples. Because of the uniformity of the bank he attributed these differences to random processes; the bank had been flooded some years previously and he considered it likely that the snail population had passed through a "bottleneck" and that small numbers of snails had founded new populations at different places along the bank which developed in divergent ways.

The samples described below came from the grass banks of railway cuttings. Four of the samples were taken from a cutting along the now disused railway line that runs south from Wingate to Stockton (see map, page 50 in the Appendix). The bank which ran south from Trimdon station was approximately 1200 metres long and was reasonably uniform; its slope was about 45°, it was 5-8 metres high, and faced due west along its entire length. The samples were taken at 250 metre intervals, Sample A being taken in Trimdon station and the rest to the south of this; ~~and~~ at each site the vegetation was very similar (see Page 49 Appendix). Each ~~one~~ site was separated by a road bridge that crossed the cutting. Unfortunately snails became very scarce along other ~~em~~bank~~ment~~s to the north and south of the one described and the only other sample obtained came from a small cutting north of Station Town (see map).

The differences between the four samples (which are classified in Tables 1, 2, 3 in the Appendix) are shown graphically in Fig. 4. They cannot be compared in detail statistically, since certain morphs are present in some of the samples, but absent in others, but by grouping these morphs with others according to colour the four samples were compared using a 2x2 Chi-squared test. At Sites A, B and C the yellow banded morph (with normal dark brown bands) was the most predominant, and at site D pink banded and yellow banded snails were equally abundant. Small numbers of pink and yellow snails with dotted light brown bands (Var. punctata Moq) occurred at sites A, B, C and D and together formed

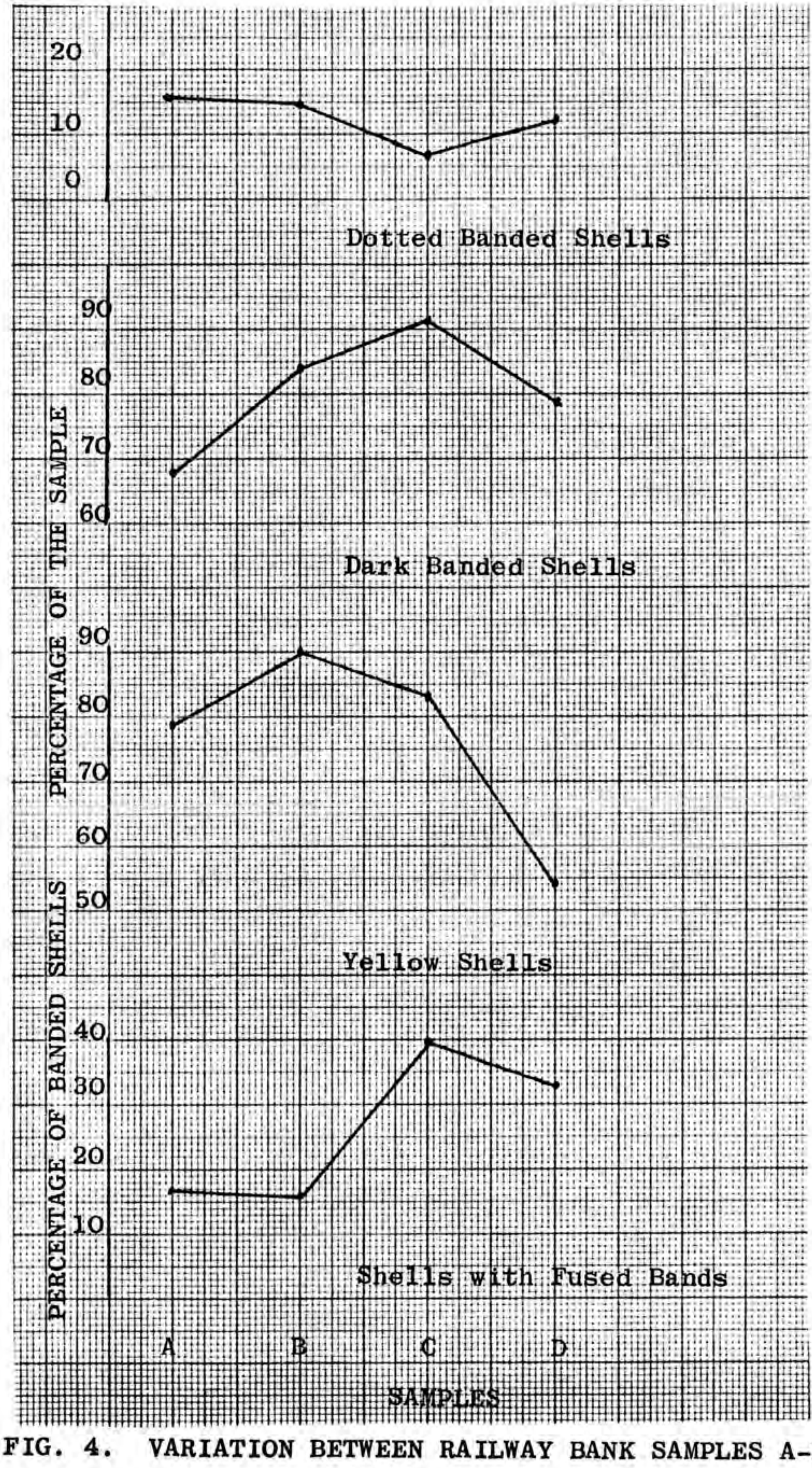


FIG. 4. VARIATION BETWEEN RAILWAY BANK SAMPLES A-D

16, 15, 7 and 12 per cent of the respective samples. Unbanded shells were scarce in samples A, C and D and absent in B, but the latter was a small sample. There was a lot of variation in the abundance of snails along the bank, at Site A they were very abundant and at the other sites they were scarce or moderately abundant. The sample at site B took about 5 hours to collect. Sites B, C and D were in the part of the cutting that ran through fields, while above site A there were houses. Perhaps some component in the water draining from the fields, for instance a pesticide, was affecting the snails.

A 2x2 Chi-squared test in which the scarce morphs were grouped with the pink and yellow banded morphs by colour showed samples A, B and C to be insignificantly different from each other but significantly different from sample D ($P<.001$ in each case). There was no apparent ecological difference between site D and the others.

The bank opposite to the one sampled was extensively burnt and few snails were to be found there. Burning provides a possible explanation for the difference between site D and the others. Before the railway was closed down (about 15 years ago) and perhaps afterwards, the east facing bank has been recently burnt, it is possible that various parts of the bank sampled were burnt, and the snails destroyed. When the burnt area recovered, a new population of snails could have grown up from a few founders and diverged from the population further along the bank. Migration is probably slowed down by the bridge which cut into the bank and in any case C. nemoralis migrates extremely slowly (Goodhart 1962).

The similarity between samples A, B and C especially between A and C, two reasonably large samples, suggests either that selection is acting to favour a particular population structure, characterised by a high frequency of yellow banded shells or that the area between sites A and C has been untouched for long enough to allow mixing of different populations or the spread of a single population, the structure of which is no more adapted to the habitat than is that of the population at site D. There is no evidence to distinguish between these two possibilities, and no evidence to show whether the snail populations along the bank are stable or unstable.

The fifth sample (Sample E) taken from another cutting, contained a high proportion of single banded snails (00300) (see Table 3) and in this respect was obviously different from the four samples described above. But with respect to the proportions of pink and yellow banded snails (there were no unbanded snails found) a 2x2 Chi-squared test showed sample E to be significantly different from samples A, B and C ($P=.01$) but insignificantly different from D. Sites D and E share no such obvious similarities not shared by the other sites and the only difference between E and all the others is that it faces North.

Because they are reasonably uniform and continuous habitats, railway banks provide an interesting habitat from which to sample *Cepaea*. The possibility that fire could have destroyed areas of the bank at different times creates opportunities for founder populations to recolonise these areas; and the degree and stability of any divergence between neighbouring populations provides some indication as to the importance of selection in determining the frequencies of the different morphs.

DISCUSSION

The polymorphism of Cepaea nemoralis is probably maintained on a physiological basis, involving heterosis (Ford 1969). The ecological genetical problem is to discover the factors responsible for altering the frequencies of the various morphs in different situations, and the relative importance of adaptation to external selective pressures, and drift.

Among the samples collected from scrub grassland habitats there was a good deal of variation despite the apparent similarity between the habitats. One characteristic shared by many of the samples was the absence or low frequency of unbanded snails, a result in agreement with the work of Cain and Sheppard on the importance of predation in determining morph frequencies. But apart from the anomalous predation results already discussed, the predation theory does not seem to explain all the differences observed. For example, at Wingate Site 1 30% of the snails collected were unbanded, although the number of predated shells found near the site suggests that predation is relatively intense there, while at the Garage quarry site no predated shells were found, but the sample collected consisted entirely of banded snails. Between many of the samples from Wingate and elsewhere there was considerable variation in the frequencies of the various banding patterns, and in the proportions of pink and yellow snails.

An important difficulty that arises when comparing Cepaea populations is that the comparison of the habitats in which they are found is not completely objective. The number of unseen differences between, for instance, Wingate site 6 and the Garage quarry site with respect to microclimate, presence of predators and parasites etc., could well be numerous. It is partly because of this that Cain (1962) has suggested that those characters or variation patterns that have been described as non-adaptive or random should properly be described as un-investigated. Cain and Currey (1963) state - "... the interaction of selective forces is complex and seems to leave little scope for merely random effects. ..." But Goodhart (1962) has quite convincingly shown that the variation he found within a population of Cepaea could be the result of random processes.

In discussing Goodhart's results on the C. nemoralis population along the Hundred Foot Bank, Cain and Currey point out that the considerable variation in the density of Cepaea along the bank suggests corresponding ecological variation and that the difference between the samples taken from the bank may be a reflection of this. On the other hand, Goodhart found that the samples from along the bank varied in a similar way to those he took from corresponding positions along a roadside verge on the far side of a road running by the side of the bank, although the verge and the bank showed consistent ecological differences. The variation between opposite samples, from the bank and verge, was usually much less than that along the whole length of either habitat, despite the reasonable uniformity of each habitat within itself. Unless unseen differences are more important than those clearly visible, the close proximity of Cepaea habitats appears to be more important in determining similarity than ecological factors held in common.

The variation along the bank, Goodhart suggests is the result of internal genotypic selection (perhaps for heterosis) acting on the differences that originally arose due to random assortment in small panmictic groups of snails, left after a previously large population passed through a "bottleneck" caused by floods in 1947.

It was suggested earlier on that the pattern of variation between the samples of Cepaea from the Wingate quarry sites 1, 2, 3, 4 and 5 is due to the quarry tip having been colonised by Cepaea from populations on either side of it. How long the snails have occupied the banks of the tip is hard to say, perhaps 10 years would not be an overestimate, especially in view of the fact that the snails from site 3 on top of the bank have had time to diverge significantly with respect to banding patterns from sites 2 and 4. The statistically significant differences between samples 2 and 4, and their respective similarity to samples 1 and 5, show that selection for a population structure suited to the bank environment has not yet obliterated the characteristics derived from the postulated parent populations. What is especially interesting about this situation is that it can reasonably be assumed that the differences between samples 2 and 4 do not reflect ecological differences between the respective sites, since it is extremely unlikely that sites 4 and 5 are more alike as far as Cepaea is concerned than are sites 2 and 4. That the differences have remained up till now could be taken as support for Goodhart's ideas on internal genotypic selection (acting on founder populations from sites 1 and 5). On the other hand, they could merely indicate that snails migrate between sites 1 and 2, and 4 and 5 in greater numbers than they migrate between sites 2 and 4. There are three reasons for supposing that migration is very restricted. Firstly, Goodhart (1962) has shown that Cepaea nemoralis moves approximately 3 yards per year (which, of course, can be in any direction). Secondly, and this seems the most convincing evidence, snails from sites 2 and 3 are significantly different with respect to banding patterns although the two sites are separated by an area of scrub grassland only 22 metres across. Thirdly, the tip is surrounded by a path of limestone rock and dust which is devoid of vegetation and might well act as a partial barrier to migration. Thus sites 4 and 5 are the same distance apart as sites 2 and 3, but the area of separation includes the path, which is at least 3 metres wide, on this side of the bank. Unless selection eventually changes part or all of the tip population, the differences now existing may be evened out in time by random movements of the snails, although Goodhart (1963) has suggested that variation due to divergent internal genotypic selection could become stabilised if cross-matings produced relatively inviable hybrids; however, this is open to question and Cain and Currey are of the opinion that if gene flow can occur, differences will eventually be evened out unless selection is operating to maintain them. It would be interesting to see how the snail population on the tip developes.

Random processes could have played a part in creating the differences observed between the other quarry samples collected. The small areas of scrub grassland found round the edges of quarries provide suitable habitats for Cepaea where perhaps none existed before the quarries were started. It is obviously possible that differences between the populations that first colonised these areas could have produced permanent differences; for instance the absence of unbanded snails at the Garage quarry site could be due to the appropriate gene never having found its way there. If unbanded snails were introduced into this site as an experiment, and became established, this would show such an explanation to be plausible.

If the area existing before a quarry was started was a suitable *Cepaea* habitat then the reduction of the suitable habitat to small areas around the edge, some of which are partially or completely isolated from neighbouring areas would provide opportunities for drift of the kind postulated by Sewall Wright (1931), to occur. In small populations (300 animals or under) random changes may occur due to sampling errors between one generation and the next unless selection is strong enough to counteract this. As the numbers of snails present in the areas sampled are not known, this suggestion is only very tentative.

Random processes have been emphasised in this discussion because the results show how they might have played a part in creating differences between populations of *C. nemoralis* and not because selection is considered unimportant.

SUMMARY

1. The differences between samples of *C. nemoralis* taken from areas of scrub grassland were described, and the possibility that random processes have played a part in creating these differences was discussed.

2. Predated shells collected from anvils near the sites sampled were compared with the respective samples. In general, banded shells appeared to be predated relatively more than unbanded, a result in opposition to the idea that unbanded shells, because they are more conspicuous against the broken background provided by scrub grassland, should be more heavily predated.

3. Where possible, young and adult snails were compared, but in no sample were they found to be significantly different. Trends indicated by a percentage analysis were discussed.

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APPENDIX

TABLE 1

Samples classified by Banding. Juveniles shown in Brackets.

Sites	12345	12345 Dotted	(12)345	1(23)45	123(45)	(123)45	(12345)	(12)3(45)	1(23)(45)	(123)(45)	10345	12045	02345	00345	00340	00300	00000	TOTAL
QUARRIES																		
Wingate																		
1	28(88)		2	2	24	1		4	2	6	(5)	1					39(70)	271
2	22(18)				22	(1)	5	13(2)		8	1(2)		2(2)			1	77(28)	193
3	10(30)		1	2	20(21)		3(8)	29(13)		18(6)		1	1				73(67)	303
4	19(69)			1(1)	2(4)			1(1)	1	(1)	(1)	(1)				(5)	26(72)	222
5	42(33)				2(1)				1					3(3)		1(4)	33(86)	167
6	7(23)				2(3)			3(2)		5(2)							46(54)	155
7	10(18)		4(4)	(1)	4(1)	1		19		1	(2)	(2)					8(8)	82
Garage	11(8)		3		2			24(5)		5(3)	1					21(9)		95
Coxhoe 1	6(4)		2		8(4)	1	16(2)	10 6	2	32(4)						12(1)		109
Coxhoe 2	7(28)				5(6)	2(1)	2(3)	7(14)		9(10)						18(18)	(1)	132
Bishop M'ham	23(4)	2		2(1)	1		(1)	9(1)		3					1*		30(4)	82
B1283	3	9			1	23*	5	22*		8		1*				5		41
Trimdon	36(19)	5	1(2)		9	1	1 (1)	10(1)	1	17 4	(1)					28(11)		144
Railway Cutting																		
A	87(57)	17(4)	1		11(8)	1		10(3)			(2)		16*(3)*		1*(1)*		21(14)	272
B	29(5)	8			1			3(2)		1								52
C	24(45)	4(2)	1	(1)	7	1	3(2)	5	2(1)	6			2*			3(4)	(1)	112
D	23(10)	6(3)	1	1	3	1	2	2	2	4						4	4(1)	68
E	9	3			3					4			3*			15		37

* With Dotted Band.

TABLE 2

Samples Classified by Morph Types - Adults and Juveniles

	NUMBERS IN SAMPLE							PERCENTAGES					
Site	Pink Unbanded	Yellow Unbanded	Pink Banded	Yellow Banded	Pink Dotted Banded	Yellow Dotted Banded	TOTAL	Pink Unbanded	Yellow Unbanded	Pink Banded	Yellow Banded	Pink Dotted Banded	Yellow Dotted Banded
Wingate													
1	38	71	93	70	0	0	272	14.0	26.2	34.4	25.5		
2	31	63	69	30	0	0	193	16.1	32.8	36.0	15.1		
3	57	83	107	56	0	0	303	18.7	27.4	35.3	18.5		
4	29	89	52	52	0	0	222	13.1	40.1	23.4	23.4		
5	14	61	35	57	0	0	167	8.4~~1~~	36.6	21.0	34.2		
6	47	54	46	8	0	0	155	30.3	34.8	29.7	5.2~~1~~		
7	5	11	38	28	0	0	82	6.1	13.4	46.4	34.2		
Garage	0	0	30	65	0	0	95			31.6	68.4		
Coxhoe 1	0	0	39	70	0	0	109			35.8	64.2		
Coxhoe 2	0	0	70	61	0	0	132			52.6	46.6		
Bishop Middleham	15	19	32	13	3	0	82	18.3	23.2	39.0	15.8	3.6	
B1283	0	0	20	6	10	5	41			48.7	14.61	24.4	12.2
Trimdon	0	0	39	100	2	3	144			27.1	69.5	1.4	2.1
Railway Cutting A	4	31	32	162	18	24	271	1.5	11.4	9.55	58.7	6.6	9.5
B	0	0	1	45	5	3	54				84.6	9.6	5.8
C	1	2	12	89	2	6	112	.9		13.4	78.5	1.8	5.4
D	2	3	29	27	2	7	70	2.9	4.4	39.7	39.7	2.9	10.3
E	0	0	12	19	6	0	37			32.4	51.3	16.2	

TABLE 1

Samples classified by Banding. Juveniles shown in Brackets.

Sites	12345	12345 Dotted	(12)345	1(23)45	123(45)	(123)45	(12345)	(12)3(45)	1(23)(45)	(123)(45)	10345	12045	02345	00345	00340	00300	00000	TOTAL
QUARRIES																		
Wingate																		
1	28(88)		2	2	24	1		4	2	6	(5)	1					39(70)	271
2	22(18)				22	(1)	5	13(2)		8	1(2)		2(2)			1	77(28)	193
3	10(30)		1	2	20(21)		3(8)	29(13)		18(6)		1	1				73(67)	303
4	19(69)			1(1)	2(4)			1(1)	1	(1)	(1)	(1)				(5)	26(72)	222
5	42(33)				2(1)				1					3(3)		1(4)	33(86)	167
6	7(23)				2(3)			3(2)		5(2)							46(54)	155
7	10(18)		4(4)	(1)	4(1)	1		19		1	(2)	(2)					8(8)	82
Garage	11(8)		3		2			24(5)		5(3)	1					21(9)		95
Coxhoe 1	6(4)		2		8(4)	1	16(2)	10 6	2	32(4)						12(1)		109
Coxhoe 2	7(28)				5(6)	2(1)	2(3)	7(14)		9(10)						18(18)	(1)	132
Bishop M'ham	23(4)	2		2(1)	1		(1)	9(1)		3					1*		30(4)	82
B1283	3	9			1	23*	5	22*		8		1*				5		41
Trimdon	36(19)	5	1(2)		9	1	1 (1)	10(1)	1	17 4	(1)					28(11)		144
Railway Cutting																		
A	87(57)	17(4)	1		11(8)	1		10(3)			(2)		16*(3)*		1*(1)*		21(14)	272
B	29(5)	8			1			3(2)		1								52
C	24(45)	4(2)	1	(1)	7	1	3(2)	5	2(1)	6			2*			3(4)	(1)	112
D	23(10)	6(3)	1	1	3	1	2	2	2	4						4	4(1)	68
E	9	3			3					4			3*			15		37

* With Dotted Band.

TABLE 3

Classification of adult snails by Colour and Banding

(Dotted Banded Morphs included with Normal Dark Banded)

	PINK									YELLOW								
Site	00000	00300	12345	123(45)	(12)3(45)	(123)(45)	Others with fusions.	One or more bands missing. No fusions.	TOTAL	00000	00300	12345	123(45)	(12)3(45)	(123)(45)	Others with fusions.	One or more bands missing. No fusions.	TOTAL
Wingate																		
1	15		20	14		2	3		54	24		8	10	4	4	4	1	55
2	28	1	13	19	9	6	3	2	81	49		9	3	4	2	2	1	70
3	28		6	18	18	11	3	2	86	45		4	2	11	7	3		73
4	5		7	2			1		15	21		12		1		1		35
5	6		18			1			25	27	1	24	2			1	3	58
6	26		7	1	2	4			40	20			1	1	1			23
7	1		9		10	1	4		25	7		1	4	9		1		22
Garage		5	3	1	12	3			24		16	9	1	12	2	3	1	44
Coxhoe 1		5	2	1	5	14	5		32		7	4	7	5	18	15		56
Coxhoe 2		8	4	2	1	6	3		24		10	3	3	6	3	1		26
Bishop M'ham	14		19	1	5	3	2	1	45	16		6		4				26
B1283		5	7			7	7		26			5	1	2	1	1		10
Trimdon		9	10	2	4	3			28		19	31	7	6	14	4		81
Railway Cutting																		
A	4		27		1			6	38	17		77	11	9		4	11	129
B			5						5			31	1	3	1	2		38
C	1		4	1		1	1	1	9		3	24	6	5	5	5	3	51
D	2	2	18	1	1	1	2		27	2	2	11	2	1	2	6		26
E		5	6	2		2		3	18		10	6	1		2			19

TABLE 5

Predated Shells Classified by Morph Types

	NUMBERS					PERCENTAGES			
Site	Pink Unbanded	Yellow Unbanded	Pink Banded	Yellow Banded	TOTAL	Pink Unbanded	Yellow Unbanded	Pink Banded	Yellow Banded
New Shells.									
Wingate Site 1									
Anvil 1	10	14	37	19	80	12.5	17.5	46.3	23.7
Site 1 Total new shells	14	24	54	31	123	11.4	19.5	43.9	25.2
Old Shells.									
Wingate Site 1									
Anvil 1	38	50	107	50	245	15.5	20.4	43.7	20.4
Anvil 2	70	63	153	64	350	20.0	18.0	43.7	18.3
Anvil 3	13	12	46	26	97	13.4	12.4	47.4	26.8
Anvil 4	11	26	52	37	126	8.7	20.6	41.3	29.4
Site 3	11	21	27	13	72	15.3	29.2	37.5	18.0
Site 5	14	50	42	48	154	9.01	32.4	27.3	31.2
Coxhoe 1			44	75	119			37.0	63.0
Coxhoe 2			11	7	18			61.1	38.9
Bishop Middleham	34	29	67	25	155	21.9	18.7	43.3	16.1
Trimdon			9	34	43			20.9	79.1
B1283			11	3	14			78.6	21.4

TABLE 6

Classification of Predated Shells by Colour and Banding

	PINK									YELLOW								
Site	00000	00300	12345	One or more bands missing. No fusions.	123(45)	(12)3(45)	(123)(45)	Others with fusions.	TOTAL	00000	00300	12345	One or more bands missing. No fusions.	123(45)	(12)3(45)	(123)(45)	Others with fusions.	TOTAL
New Shells Wingate Site 1																		
Anvil 1	10		22		6	7	2		47	14		6		5		5	3	33
Anvil 2	1		1			1	1		4	2		1				1	1	5
Anvil 3	1		2				4	1	8	3		2			2	1		8
Anvil 4	2		6				1		9	5		3		1				9
TOTAL	14		31		6	8	8	1	68	24		12		6	2	7	4	55
Old Shells Wingate Site 1																		
Anvil 1	38		53	2	17	20	7	7	144	50		21		7	5	10	7	100
2	70		68	1	30	23	22	9	223	63		29		7	13	12	3	133
3	13		22		5	8	9	2	59	12		13		4	4	5		28
4	11	2	36		1	2	3	4	59	26	1	25		1	4	1	3	61
TOTAL	132	2	174	3	53	53	41	22	485	151	1	88		19	26	28	13	322
Wingate																		
Site 3	11		2	1	5	11	4	4	38	21		4		3	6			34
Site 5	14	1	36			1		4	56	50	2	33		4	4		5	93
Coxhoe 1		2			4	6	23	7	42		4	5	1	4	13	4	24	55
Coxhoe 2		3	3			1			7		4	1		1	2	3		11
Bishop M'ham	28	1	50		1	7	9	6	103	34		14	1	1	6	1	3	60
Trimdon		4	3			1	1		9		10	14		3	1	5	1	34
B1283		3	2				3	2	10			2				1	1	4

TABLE 7

Samples and Predated Shells classified according to Postulated Conspicuousness to Predators

	NUMBERS IN SAMPLE				PERCENTAGES		
Site	Effectively Banded	Inter-mediate (Fusions among first three bands)	Effectively Unbanded. All shells with first 2 bands missing.	TOTAL	Effectively Banded	Intermediate	Effectively Unbanded
A. Predated Shells. New Shells.							
Wingate Site 1 Anvil 1	89	17	24	80			
Total New Shells.	55	30	38	123			
Old Shells. Wingate. Site 1							
Anvil 1	98	58	89	245			
Anvil 2	134	83	133	350			
Anvil 3	44	28	25	97			
Anvil 4	63	19	44	126			
TOTAL	339	188	291		41.4	22.9	35.6
Site 3	14	25	33	72	19.4	34.7	45.8
Site 5	73	17	64	154	47.4	11.0	41.6

Table 7 cont'd/

TABLE 7 (continued)

Coxhoe 1	13	100	6	119	10.9	84.0	5.1
Coxhoe 2	5	6	7	18	27.8	33.3	38.9
Bishop Middleham	66	32	64	155	40.7	19.8	39.5
Trimdon	20	9	14	43	46.5	20.9	32.6
B1283	4	7	3	14			
B. <u>The Samples. (Adults Only)</u>							
Wingate							
Site 1	53	17	39	109			
Site 3	31	53	73	157			
Site 5	44	3	37	84			
Coxhoe 1	14	63	12	89	15.7	70.8	13.5
Coxhoe 2	12	20	18	50	24.5	40.0	36.0
Bishop Middleham	26	14	30	70	37.1	20.0	42.9
Trimdon	52	31	28	111	46.8	27.9	25.3
B1283	13	22	5	40			

TABLE 8

Values of Chi-Squared

Predation

Heterogeniety among old predated shells from anvils around site 1 Wingate:

(a) For the four morph types $^{2}_{(9)}$ = 15.3

(b) For the three classes, effectively banded, intermediate, effectively unbanded $^{2}_{(6)}$ = 11.9

Site	Comparison of predated shells and sample	
	For the four morph types	For the effectively banded, intermediate and effectively unbanded classes
Wingate		
Site 1 New shells anvil 1	$\chi^{2}_{(3)}$ 4.6	$\chi^{2}_{(2)}$ 1.2
Site 1 New shells Total	4.0	2.6
Old Shells		
Site 1 (Total)	12.3	3.2
Site 3	.45	^{2} = .1
Site 5	.9 (2 morph types)	5.9
Coxhoe 1	.03	6.2
Coxhoe 2	.81	3.9
Trimdon	1.3	1.1
Bishop Middleham	1.6	.2

TABLE 9

Values of CHI-Squared. Comparison of Samples

Samples	Comparison with respect to the four morph types	Comparison with respect to banding pattern
Wingate	χ^2	χ^2
1,2	(3) 7.3	(6) .68
1,3	5.8	14.3
1,4	8.44	11.5
1,5	10.93	29.4
1,6	39.2	.02
1,7	11.6	2.2
2,3	2.2	8.7
2,4	10.7	> 10.8
2,5	24.0	> 10.8
2,6	17.3	10.1
2,7	23.2	.46
3,4	16.3	> 10.8
3,5	28.9	> 10.8
3,6	21.8	> 10.8
3,7	20.9	.63
4,5	6.28	2.24
4,6	34.6	> 10.8
4,7	28.7	> 10.8
5,6	55.4	> 10.8
5,7	22.5	> 10.8
6,7	57.0	.67
Bishop Middleham, Wingate Site 1		
Garage, Coxhoe 1	χ^2 (1) .23	χ^2 (16) > 40
Garage, Coxhoe 2	9.7	
Garage, Trimdon	-.13	
Garage, B1283	18.4	
Coxhoe 1, Coxhoe 2	6.8	
Coxhoe 1, Trimdon	19.9	
Coxhoe 1, B1283	15.3	
Coxhoe 2, Trimdon	13.0	
Coxhoe 2, B1283	4.20	
Trimdon, B1283	25.1	
Railway Cutting		
A,B	χ^2 (1) 2.2	χ^2 (1) .4
A,C	2.7	11.1
A,D	21.5	5.6
A,E	18.6	23.5
B,C	1.2	10.5
B,D	16.8	6.4
B,E	18.0	> 10.8
C,D	23.5	.28
C,E	25.7	2.36
D,E	1.3	4.58

TABLE 10

Comparison of Young and Adult Snails

Percentages

Site		Pink banded shells		Yellow banded shells	
		Young	Adults	Young	Adults
Wingate	1	30.4	34.4	28.0	25.5
	2	26.4	36.0	20.8	15.1
	3	34.0	35.3	20.0	18.5
	4	23.7	23.4	23.1	23.4
	5	19.0	21.0	31.0	34.2
	6	29.4	29.7	5.9	5.16
	7	40.0	46.4	37.1	34.2
Coxhoe	1	28.6	37.5	71.4	62.5
Coxhoe	2	56.7	48.0	43.3	52.0
Trimdon		31.5	27.4	68.5	72.6
Garage quarry		24.0	34.3	76.0	65.7

		Banded shells		Yellow unbanded shells	
		Young	Adults	Young	Adults
Wingate	1	58.3	62.5	28.0	26.2
	2	47.1	52.0	28.3	32.8
	3	53.8	53.8	26.2	27.4
	4	43.9	48.0	39.3	40.1
	5	50.6	60.7	40.5	36.6
	6	35.3	28.1	40.0	34.8
	7	77.1	81.0	11.4	13.4

		Pink unbanded shells	
		Young	Adults
Wingate	1	13.7	14.0
	2	24.5	16.0
	3	20.0	18.7
	4	13.9	13.1
	5	9.5	8.7
	6	24.7	30.3
	7	11.4	6.1

TABLE 11

Values of Chi-squared for Comparisons of Young and Old Adult Snails

Site	Chi-Squared	
Wingate 1	$\chi^2_{(3)}$	3.3
2		6.7
3		.8
4		4.46
5		1.7
6		3.5
7		Numbers too small
Garage quarry	$\chi^2_{(1)}$	.49
Coxhoe 1		.2
Coxhoe 2		.6
Trimdon		.1

PLANT SPECIES IN THE AREAS SAMPLED

WINGATE

Sites 1, 2, 3, 4, 6, 7

Grasses

Dactylis glomerata
Holens lanatus
Arrhenatherum elatior
Festuca sp.
Briza media

Other Species

Heracleum sphondylium
Centaurea nigra
Siccisa columbera
Primula veris
Campanula rotundifolia
Lotus corniculatus
Poterium sanguisorba
Plantago lanceolata
Achillea millefolium
Vicia cracca
Rananculus acris
Trifolium repens
Trifolium pratense
Rubus sp.
Orchis fuchsii
Galium verum
Tussilago farfara

Site 5

Grasses

Phalaris arundinacea
Dactylis glomerata

Other Species

Urtica disica
Filipendula ulmaria
Heracleum sphondylium
Daucus carota
Lathyrus pratense
Chamaenerion angustifolium
Rubus sp.
Circium arvense

Garage Quarry

Grasses

D. glomeratus
B. media
A. elatior
Festuca sp.

Other Species

H. sphondylium
C. nigra
S. columbera
L. corniculatus
G. verum
Hieracium sp.
P. lanceolata
P. veris
D. carota
Rhinathus minor
T. pratense
Carex sp.
A. millefolium
Tragopogan pratensis
Rubus sp.
Stellaria media
Medicago lupulina
Pastinaca satira
P. sanguisorba

Coxhoe 1

Grasses

D. glomeratus
A. elatior
Festuca sp.
B. media
H. lanatus

Other Species

H. spondylium
C. nigra
S. columbera
T. officinalis
L. pratensis
T. repens
Linum sp.
V. cracca
Prunella vulgaris
M. lupulina
Senecio jacobea
Sonchus oleraceus
Odontites verna
T. farfara
P. media
Rubus sp.

The Railway Sites

Grasses

D. glomeratus
H. lanatus
B. media
Festuca sp.

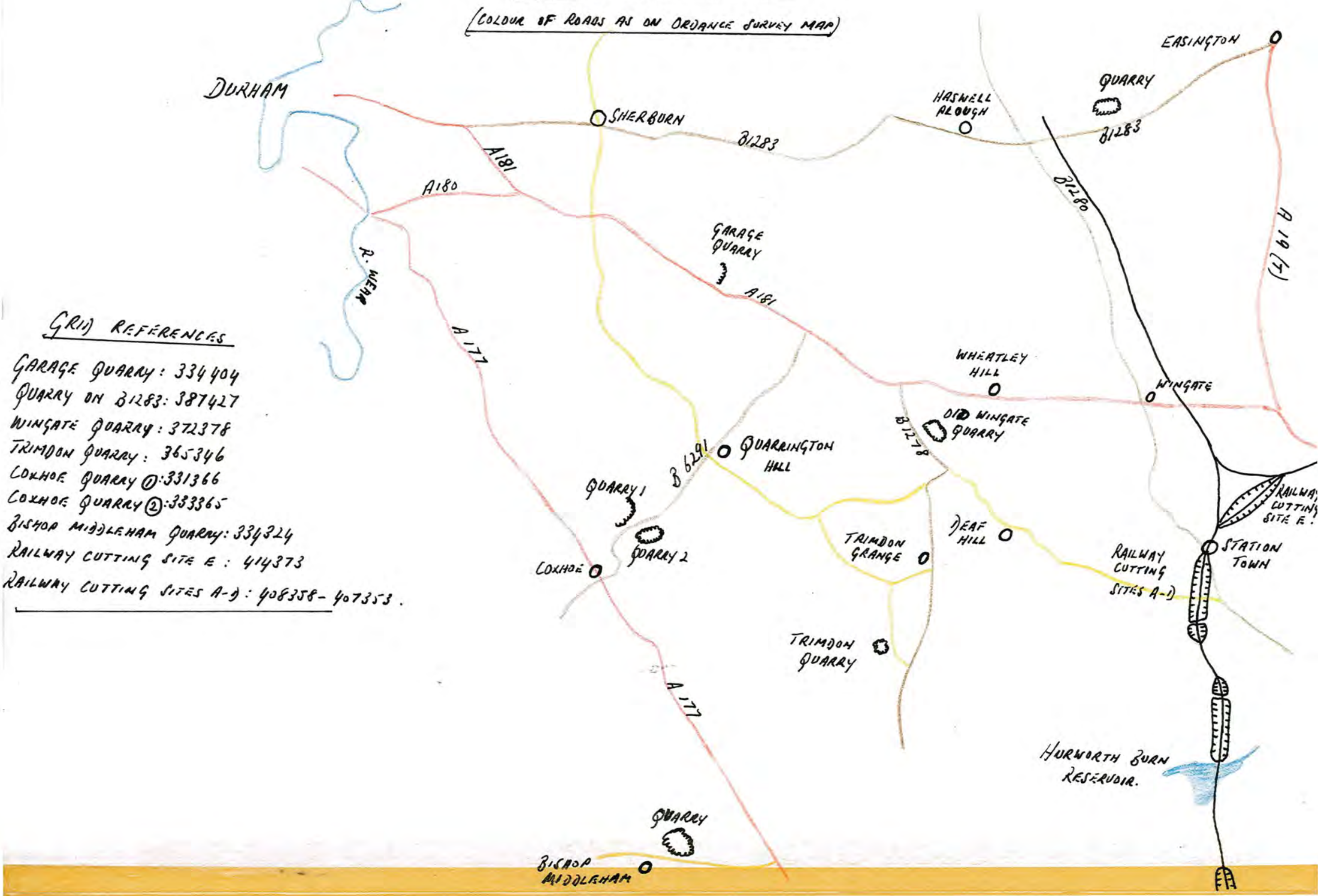
Other Species

H. spondylium
C. nigra
Leontedon sp.
Hypericum sp.
T. farfara
Equisetum
L. pratensis
D. carrota
S. columbera
T. officinalis
T. pratense
O. verna
C. arvense
Viola sp.
Rubus sp.
Carex sp.

The plant species found at the other quarry sites are not listed separately as this would be merely repetitious.

MAP OF AREA SAMPLED.

(COLOUR OF ROADS AS ON ORDNANCE SURVEY MAP)



GRID REFERENCES

GARAGE QUARRY: 334404
QUARRY ON B1283: 387427
WINGATE QUARRY: 372378
TRIMDON QUARRY: 365346
COXHOE QUARRY ①: 331366
COXHOE QUARRY ②: 333365
BISHOP MIDDLEHAM QUARRY: 334324
RAILWAY CUTTING SITE E: 414373
RAILWAY CUTTING SITES A-D: 408358-407353.

MAP OF WINGATE QUARRY SITES.