CEPAEA NEMORALIS IN BRITTANY, CORNWALL AND PEMBROKESHIRE

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1. INTRODUCTION

VISUAL selection by predators has been shown to influence shell colour and banding morph frequencies in natural populations of the land snail *Cepaea nemoralis* (Cain and Sheppard, 1950, 1954; Arnold, 1966). In some areas the resulting correspondence with background does not occur. Constant morph frequency over a large and diverse area despite visual selection has been termed an "area effect" (Cain and Currey, 1963). Climatic conditions are evidently responsible for certain area effects (Cain and Currey, 1963; Carter, 1965; Arnold, 1966, 1968), although it has been argued that random events in the past gave rise to present-day area effects (Goodhart, 1963; Guerrucci-Henrion, 1966).

Guerrucci-Henrion (1966), studying populations in Brittany, found that variation in morph frequencies could not easily be explained by visual selection. She concluded that, although shell colour morph frequency is probably influenced by humidity, the wide variation in banding frequency, and the absence of a clear relationship with environmental factors, shows the largely random nature of banding morph distribution. However, analysis of Guerrucci-Henrion's results does show increasing frequency of effectively banded morphs from north to south Brittany, reflected by decreasing midbanded frequency. Although it may be difficult or impossible to show any corresponding environmental changes, a similar pattern of variation for other westerly facing peninsulas would suggest the action of selective, rather than random factors affecting morph frequency.

This paper reports a study of natural populations of *C. nemoralis* in the peninsulas of Cornwall in south-west England, and Pembrokeshire in south-west Wales, and compares the results with those of Guerrucci-Henrion in Brittany.

2. COLLECTING

The results used here are from random samples collected in Brittany (Guerrucci-Henrion, 1966), north Cornwall (Arnold, 1966), north and south Cornwall (collected by Miss A. M. Kirkby, J. S. Jones and myself during the easter of 1967), Pembrokeshire and along the south coast of England (collected by Mrs A. M. Harvey and myself during the summer of 1969). Samples in Britain were taken from non-calcareous coastal cliff tops. Samples from Brittany were also taken from non-calcareous sites, but although the majority were coastal some were taken up to 15 km. inland. In all areas studied there is a rarity of calcareous rock, and *C. nemoralis* populations are restricted to coastal regions where there is an adequate supply of calcium. Inland, when *Cepaea* are found they tend

to be *C. hortensis*. Occasionally, in sheltered areas, *C. hortensis* is found along the coast and in these areas it often entirely displaces populations of *C. nemoralis*.

3. RESULTS

Samples were scored by the methods of Cain and Sheppard (1950, 1954). Scores and details of sample sites from my own samples are available elsewhere (Harvey, 1970). The areas sampled are shown in fig. 1. Samples

FIG. 1.—The areas considered in the general comparison are shown enclosed (l.e. = Land's End; c.b. = Chesil Beach).

from Brittany and Pembrokeshire are classified into one of three areas—north, west or south. As Cornwall has no west coast it is divided into north and south.

In all areas the situation is similar with respect to morphs present. The vast majority of snails are either unbanded, mid-banded or five-banded, and almost all populations contain the yellow and pink morphs. Brown snails were only found in four samples taken in the extreme south of Cornwall. The white-lipped form is only found in Cornwall, and here it is more common in the north than the south.

Histograms of effectively banded morph frequency for Cornwall and Pembrokeshire are compared with those for Brittany (from Guerrucci-

FIG. 2.—Effectively five-banded morph frequency histograms for each area. The number of samples is shown on the abscissa and morph frequency on the ordinate.

Henrion, 1966) in fig. 2. There is an increase in frequency from north to south in all cases, reflected to a certain extent by a decrease in mid-banded morph frequency (fig. 3). Although variable, unbanded morph

frequency shows no difference between north and south in any area. There is a significant decrease in yellow morph frequency from north to south

FIG. 3.—Mid-banded morph frequency histograms for each area. The number of samples is shown on the abscissa and morph frequency on the ordinate.

Brittany, but no corresponding shift in Pembrokeshire or Cornwall. The results of median tests on morph frequency histograms are summarised in table 1.

TABLE 1

Median test between north and south. Values are of chi-squared with one degree of freedom

	Unbanded	Mid-banded	Effectively banded	Yellow
Cornwall	1.2 ns	9.4**	13.1***	0.01 ns
Pembrokeshire	2.0 ns	5.0*	9.8**	1.8 ns
Brittany	2.3 ns	4.1*	13.5***	35.5***

White lipped between north and south Cornwall 9.1*.

4. DISCUSSION

Colour

The lack of change in shell colour morph frequencies between north and south Cornwall and Pembrokeshire does not imply that the same selective forces are not acting in Brittany, Cornwall and Pembrokeshire. Guerrucci-Henrion produced evidence that yellow morph frequency decreases in areas of higher rainfall in Brittany. As the coasts of Cornwall and Pembrokeshire follow the 40-inch isohyet we would, on the hypothesis that rainfall influences shell colour morph frequency, expect no change in yellow morph frequency from north to south of either region. However, although there is no difference in yellow morph frequency between north and south Pembrokeshire, or north and south Cornwall, we would also expect that yellow morph frequency would be the same in both regions. This is not so. The mean yellow morph frequency in Cornwall (68 per cent.) is 19 per cent. higher than in Pembrokeshire (49 per cent.). In Brittany, where rainfall is lower, yellow morph frequency is comparable with these values (north 32 inches, 62 per cent.; west 36 inches, 58 per cent.; south 26 inches, 42 per cent.). Furthermore, samples taken along the south coast of England, east from Land's End to the Chesil Beach (see fig. 1), where rainfall shows a decrease from 40 inches to about 31 inches, show a significant *decrease* in yellow morph frequency (see fig. 4). From these results, therefore, there is no evidence that rainfall influences shell colour morph frequencies in the areas considered. Comparison of shell colour morph frequencies with other climatic variables such as humidity, maximum, minimum or mean temperatures does not indicate factors influencing morph frequencies. Arnold (1966) suggested that low soil pH could influence morph frequencies in northern Cornwall, but measurement of soil pH at all sites that I sampled in north and south Cornwall as well as Pembrokeshire and the south coast of England, demonstrated no relationship between any morph frequency and pH.

Arnold, analysing his results from northern Cornwall, and Guerrucci-Henrion analysing hers from Brittany, could find no clear relationship between shell colour morph frequency and vegetational background which would indicate an influence on morph frequencies caused by visual selection by predators. It is conceivable from fig. 4 that in woodland on southern Cornish clifftops shell colour morph frequency is influenced by visual selection. The majority of variation in shell colour morph frequency in Cornwall and Pembrokeshire, at least, remains unexplained.

Banding

The repeated increase in five-banded morph frequency from north to south in the three westerly facing peninsulas suggests the action of selective forces common to all three regions. No difference in climatic variables can

FIG. 4.—Yellow morph frequency plotted east from Land's End to the Chesil Beach. Closed symbols represent woodland. Open squares represent samples with brown snails present. ($P: b \neq 0 < 0.001$.)

be found to account for this, although in Cornwall and Pembrokeshire vegetation does become less open from north to south with a predominance of open grassland in the north and woody scrub in the south (*Sarothamnus scoparius*, *Prunus spinosa* and *Rubus fruticosus*). It was considered that the change in temperature experienced by cliff slopes with differing aspects (Geiger, 1966) might account for these changes in morph frequency, but repeated sampling of opposing cliff slopes across bays showed that aspect of cliff slope bears no relation to morph frequency within an area. Predation by the song thrush (*Turdus philomelos*), measured by the amount of predated shells recovered, is more intense in the south of Cornwall and Pembrokeshire than in the north of either region. As the effectively banded morphs are

more cryptic at most sampling sites it is possible that the increase in effectively five-banded morph frequency from north to south is due to the effects of visual selection overriding some other form of selection in the south. On this hypothesis it is surprising that effectively banded morph frequency increases at the cost of mid-banded, and not both mid-banded and unbanded as the latter have approximately equal visual selective values (Cain and Sheppard, 1954).

The white-lipped form, found in Cornwall, is present only in the more exposed areas, not being found in the sheltered areas of St Ives Bay and Mounts Bay, where the cliffs are also lower. The presence of the white-lipped morph on high exposed ground agrees with the findings of both Cook (1966) and Arnold (1968), although in eastern Yorkshire the morph is not confined to high exposed areas (Harvey, in preparation).

As in Brittany, areas of significant association between shell colour and the unbanded morph are found, but again these cannot be related to morph frequency, vegetation, climate or soil pH. In Cornwall there is also evidence of areas with a disequilibrium between mid-banded and five-banded morphs within the different colour classes. White lip, when present, is normally only found in one colour morph, and in either banded or unbanded snails (Cook, 1966). Associations between morphs in Cornwall will be considered in a later paper in which two areas with unusual morph frequencies will also be examined.

5. SUMMARY

1. Coastal populations of the land snail *Cepaea nemoralis* from three westerly peninsulas are considered. Shell colour and banding polymorphisms are similar in the three areas.

2. A striking increase in effectively banded morph frequency from north to south in each area is evident, suggesting that similar selective forces are operating in all three areas.

3. There is no evidence to suggest that climatic factors influence morph frequencies.

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