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Ecological Genetics and Natural Selection in Molluscs

Climatic selection has an important effect on some patterns of gene distribution in snail populations.

J. S. Jones

Recent investigations of protein polymorphism which suggest that up to 40 percent of all gene loci may be polymorphic in animals as diverse as *Limulus* and man (1) have led to a resurgence of interest in the mechanisms which are responsible for the maintenance of genetical variation in natural populations. Ecological genetics is the study of the relationship of such variation to the environment. Unfortunately, much research which is intended to refer to the ecological genetics of a system suffers from the weakness of the investigation of Chinese metaphysics by the Dickensian character who obtained his information by combining encyclopedia articles on China and on metaphysics. We have adequate information on the genetics of some organisms and on the ecology of others, but in relatively few cases is sufficient data available on both variables to justify a realistic amalgamation. Resolution of the long-standing disagreement between those who think that natural selection is the main factor affecting genetic variation in natural populations and those who emphasize the importance of random processes has therefore been delayed by a lack of suitable information.

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Ecology and Genetics of Land Molluscs

Polymorphic land snails are excellent material for research into the interactions of ecology and genetics. Individual species may live in a wide range of environments, their shells can easily be marked for identification, and empty shells (whose appearance may give an indication of the cause of death) leave a record of some of the genes which the animal possessed when alive. The low mobility of most land snails also means that populations sharing a common gene pool are small and can be studied in detail. These factors make it relatively easy to study the ecology of snail populations. *Cepaea nemoralis*, a common European helioid, is the most widely investigated species. Information is now available on its food, reproduction, growth rate, survival, movement, activity, actual and effective population size, and predators (2). Much work has also been conducted on the genetics of its visible polymorphism.

The shell may be yellow, pink, or brown, and bears up to five dark or partly pigmented bands. The genes for shell color are allelic. A locus controlling the presence or absence of bands is closely linked to the color locus, and several other loci controlling

intensity of band and lip pigmentation are linked to these loci to form a "supergene." Two loci reducing the number of bands on the shell to less than five are not linked to this supergene (3).

The complexity of the visible polymorphism in *C. nemoralis* is matched by its ubiquity. I have records of only 26 monomorphic colonies out of more than 4000 sampled in Britain and France. *Cepaea hortensis*, which is closely related to *C. nemoralis*, is also highly polymorphic, and the visible polymorphism of the two species is homologous to such an extent that dominance relations are preserved in interspecies crosses (4). Polymorphism in *C. hortensis* is not as extensive as in *C. nemoralis*, 11.7 percent of British colonies being monomorphic for shell color and banding. *Cepaea sylvatica* and *C. vindobonensis* are continental European species which have considerably simpler systems of shell polymorphism. The ecology and genetics of several other molluscs have also been investigated (5).

Ecological Genetics of *Cepaea*

The extreme local variations in morph frequency found in *Cepaea* populations were for many years quoted as examples of the importance of random processes in determining population structure. On the basis of a survey of *C. nemoralis* populations in France, Lamotte (6) also concluded that genetic drift is the major factor affecting gene frequencies because he could find no associations of morph frequency with environment, and because analysis of his data suggested that they were in accordance with Wright's (7) predictions for populations whose structure is primarily determined by random processes.

More recently, however, natural selection has been shown to be important in affecting the distribution of genes in

at least some *C. nemoralis* populations. In lowland areas of southern England there is often a clear association between morph frequency and habitat type (Fig. 1). Woodland populations have a high frequency of unbanded pink and brown shells, while populations from open habitats have a correspondingly high frequency of banded yellow shells. This association of morph frequency with background is due to differential selection by predators acting against the more conspicuous shells (8). A selective advantage of the heterozygote over both homozygotes may be involved in maintaining the polymorphism against the pressure of directional selection (9), although frequency-dependent selection by predators attacking the commonest varieties might also have some local importance (10, 11).

Not all populations of *C. nemoralis* show this association with background. On chalk uplands in Britain, morph frequencies apparently bear no consistent relationship with the background upon which the snails are living, although there may be intense predation. Large areas are characterized by a limited range of morph frequencies, while in adjacent and apparently similar areas the frequencies of these morphs are quite different (Fig. 2). The transitions (clines) between each area may occur within a continuous population, do not coincide with any obvious environmental discontinuity, and are often extraordinarily steep. These "area effects" (9) represent a situation where ecologically dissimilar but geographically conjunct regions have similar morph frequencies, while ecologically similar but geographically separate regions have quite different frequencies. Area effects have now been found in many populations of *C. nemoralis* and *C. hortensis*, and the general structure of populations of these species appears to be a series of overlapping mosaics of area effects at each locus, rather than overall correspondence of morph frequency with background. Phenomena similar to the area effects in *Cepaea* exist in populations of other molluscs (5). Rather similar patterns of variation also occur in *Drosophila* (where some populations of *D. pseudoobscura* show a local constancy of karyotype in spite of a variable environment), in plants such as *Linanthus parryae* (where blue flowered individuals occur only in "variable areas" which bear no apparent relationship to ecology), and possibly in man (where geographical differentiation of blood group and other

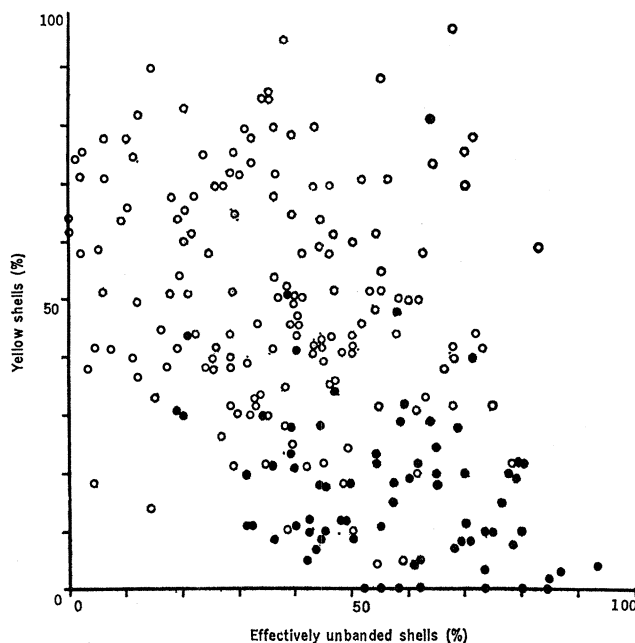


Fig. 1. Association between morph frequency and background vegetation in English populations of *C. nemoralis* in which visual selection affects color and banding morph frequencies. Symbols: closed circles, woodland populations; open circles, populations from open habitats. Effectively unbanded shells (8) lack at least the top two shell bands. Data from (8-10, 16, 38).

polymorphisms often cannot be related to the environment) (12). It is clear that area effects in *Cepaea* may prove to be of much more than specialist interest.

The mechanisms underlying this pattern of morph distribution are a matter of controversy. Random genetic drift acting currently cannot be an explanation of most area effects because the populations involved are far too large. Comparison of modern *Cepaea* populations on the surface of ancient earthworks (about 4500 years B.C.) with those buried on the original land surface suggests that morph frequencies have undergone systematic changes; this would not be expected if random processes exert a significant effect (13, 14). Several authors consider that geographical variations in gene frequency in *Cepaea* are due to environmental selection, and have suggested numerous possible selective forces. These include gross climatic differences such as mean January temperature; microclimatic variables associated with altitude, aspect, rainfall, cloud cover, frost hollows, and proximity to rivers; and geology (15-18). Endler (19) has shown that even slight environmental gradients may give rise to steep clines. In many places, however, it has not been possible to identify any environmental factor that affects morph frequency; this is certainly the case in regions of uniform topography, and may also be true in topographically variable areas (17). The Polynesian snail *Partula taeniata*, for example, shows area effects for shell color in which gene frequencies are stable from lowland forests over almost bare mountain ridges, but show rapid

transitions in an apparently uniform wood (20).

Several explanations which minimize the importance of environmental selection have therefore been proposed. These include models of founder populations with different initial gene frequencies evolving incompatible gene pools and expanding until they meet; of random processes acting in a continuous population; and of the evolution of steep clines because of the accumulation of modifying genes in a manner which cannot usually be related to the action of the environment (21). There is little direct evidence which suggests that area effects result from such differences in "genetic environment." In *Partula taeniata* a steep cline between area effects for shell color coincides with a uniquely high frequency of banded shells, with disturbances in dominance relationships, and with correlated changes in shell size and the breeding condition of the snails. Clarke (20) considers that the cline therefore probably represents a transition between two differently coadapted gene complexes, rather than a selective response to an undetected environmental factor. He suggests that reinforcement of the genetic divergence between these adjacent gene complexes may lead to "parapatric" speciation. If this process does occur, it adds a new dimension of interest to the study of area effects.

There is no generally accepted theory which explains the origin and maintenance of area effects. One method of estimating the importance of environmental selection would be to examine morph frequencies in widely separated molluscan populations which are known

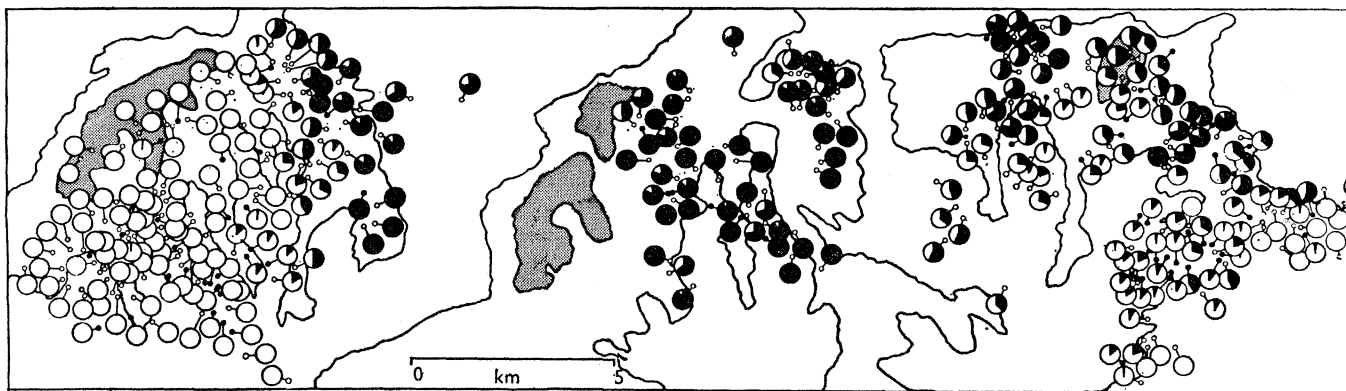


Fig. 2. Frequency of five-banded shells (black sectors) in *C. nemoralis* on the Marlborough and Berkshire Downs. Symbols: closed circles, woodland populations; open circles, populations from open habitats. Contours at 600 and 800 feet (183 and 244 meters). Note lack of association of morph frequency with background or topography. Data from (9, 16).

to be living in very different environments. Another approach is to investigate area effects involving simple polymorphic systems (such as that of the eastern European snail *Cepaea vindobonensis*) in clearly defined and contrasting microenvironments. In the remainder of this article I describe two such investigations.

Gene Frequency and Climate in *Cepaea nemoralis*

Any genes in *C. nemoralis* which do show the selective responses to local climate claimed to exist by several authors might also be expected to show changes in frequency throughout the species' range which can be correlated

with large-scale climatic trends. Previous attempts to detect such trends (9, 18, 22) have been based on insufficient data and have had limited success. Figure 3 shows morph frequency histograms based on approximately 500,000 specimens of *C. nemoralis* collected throughout Britain and Europe. There is a very clear cline in the frequency of yellow shells from the north to the south of Europe, the median frequency of this morph increasing from 39 percent to 100 percent with increasing distance from the northern limit of *C. nemoralis*' range. None of the genes controlling the number of shell bands show such regularities in their distribution.

There is a significant association of the frequency of yellow shells with

mean summer temperature ($b = 9.06$; $P < .001$) but none of the banding morphs show a convincing association with the climatic variables tested. A multivariate analysis involving the collection of more data and a more detailed investigation of climate is in preparation (23), but the results presented here indicate that climatic selection has a marked effect on at least some large-scale variations in morph frequency in *C. nemoralis*.

Ecological Genetics of *Cepaea vindobonensis*

Cepaea nemoralis has a very complex system of visible polymorphism. Even when only polymorphisms whose mode of inheritance is understood are considered, there are more than 18,000 possible shell phenotypes. *Cepaea vindobonensis* is an eastern European species with a much simpler shell polymorphism. Neither its formal genetics nor its ecological genetics has previously been studied. There is no variation in shell color, and banding polymorphism is restricted to minor variations in band number (usually four or five bands), in the degree of band fusion, and in the intensity of band pigmentation. The bands may be dark and heavily pigmented, or the pigment may be reduced to give a light straw color, which I refer to as faint banding (Fig. 4). This relative simplicity may make it correspondingly easier to detect any effect of the environment on the distribution of morph frequencies.

An investigation of *C. vindobonensis* was carried out in the Velebit Mountains of northern Yugoslavia (24). These limestone mountains were chosen for study because they possess a great deal of topographical variation which might be reflected in the snails' popula-

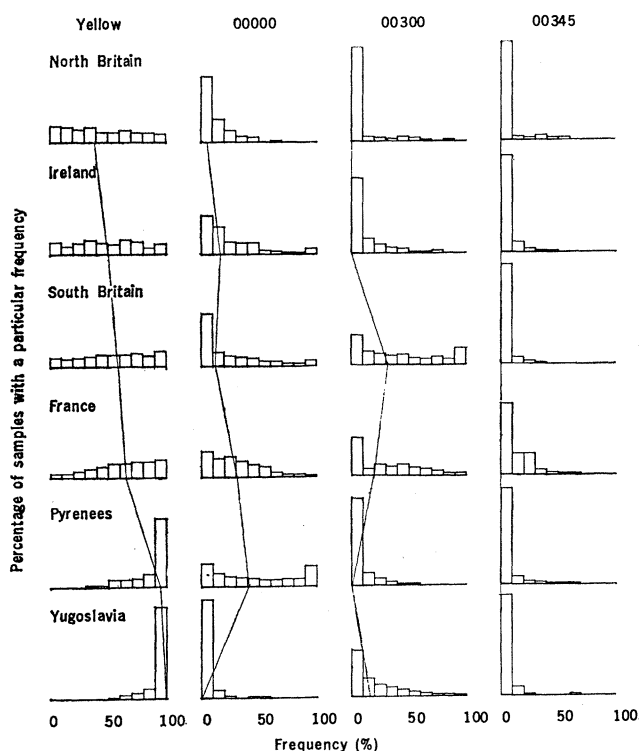


Fig. 3. Morph frequency histograms for populations of *C. nemoralis* throughout Europe; 00000, unbanded shells; 00300, central band only; 00345, lower three bands only. Vertical lines connect median frequencies in each region. Data from (6, 8-10, 15-18, 22, 26, 38, 39).

tion structure. Basins surrounded by steep mountains up to 1700 meters high are the major relief feature in the area. The floors of the basins are remarkably level, and they vary in height from 420 to 600 meters above sea level (Fig. 5). The alluvial soils found in the basins are often intensively cultivated, with many hedgerows of hawthorn and blackthorn, sometimes associated with ivy, brambles, and broad-leaved vegetation, and overhung by plum and other trees. Similar hedgerows occur on the thin soils of the mountainsides, often in association with open karst woodland or scrub made up of clumps of ash, beech, oak, and hazel. Dense beech and conifer forests are found above about 750 meters (25).

Distribution of Morph Frequencies

Cepaea is common in the basins and on the lower slopes of the surrounding mountains (up to 770 meters). *Cepaea vindobonensis* usually occurs in conjunction with *C. nemoralis* (26). Most

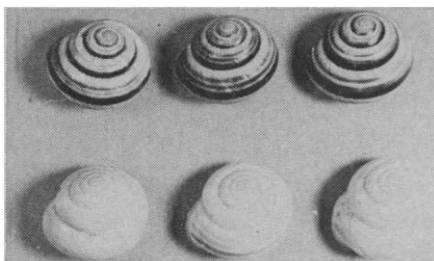


Fig. 4. Shells of *Cepaea vindobonensis* showing fully pigmented bands (top row) and faint bands (bottom row).

samples originate from hedgerows, but a few are from thickets of bramble and broad-leaved vegetation or from scrub. Each sample was taken from as small an area as possible, and all snails seen were collected and used in the analysis of morph frequencies. A total of over 15,000 snails in 400 samples was collected (27).

There are considerable geographical variations in morph frequency in *C. vindobonensis* throughout the area; these variations are most marked for the frequency of shells with faint bands

(Fig. 6). This phenotype shows intense regional localization, as it is absent from many populations but reaches high frequencies in others. Band fusions show a similar, but less extreme, degree of localization, while the frequency of shells with one band missing is low and fluctuates from sample to sample. The general pattern of morph distribution in these populations of *C. vindobonensis* is rather similar to that found in *C. nemoralis* on chalk uplands in southern England.

There is no significant association between morph frequency and background vegetation, although it is difficult to establish any correlations with background from these collections, as they originate from a limited range of vegetation types. Very few predated shells were collected. There is a very strong association between the frequency of faint banded shells and the position of the population within or outside a basin. Faint banded shells reach a high frequency (sometimes up to 100 percent) only on the steep mountain slopes around the basins, and

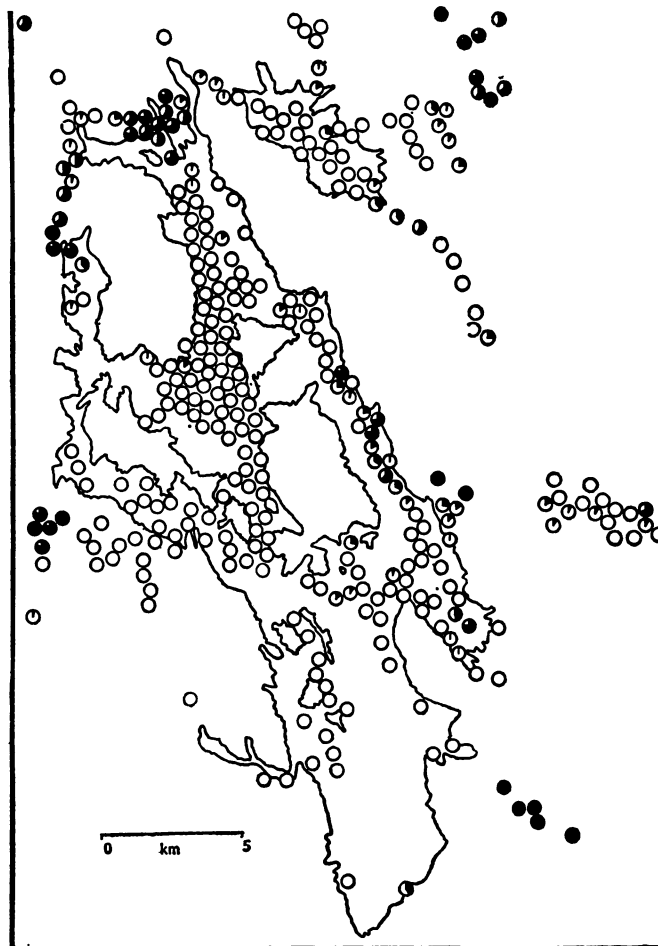
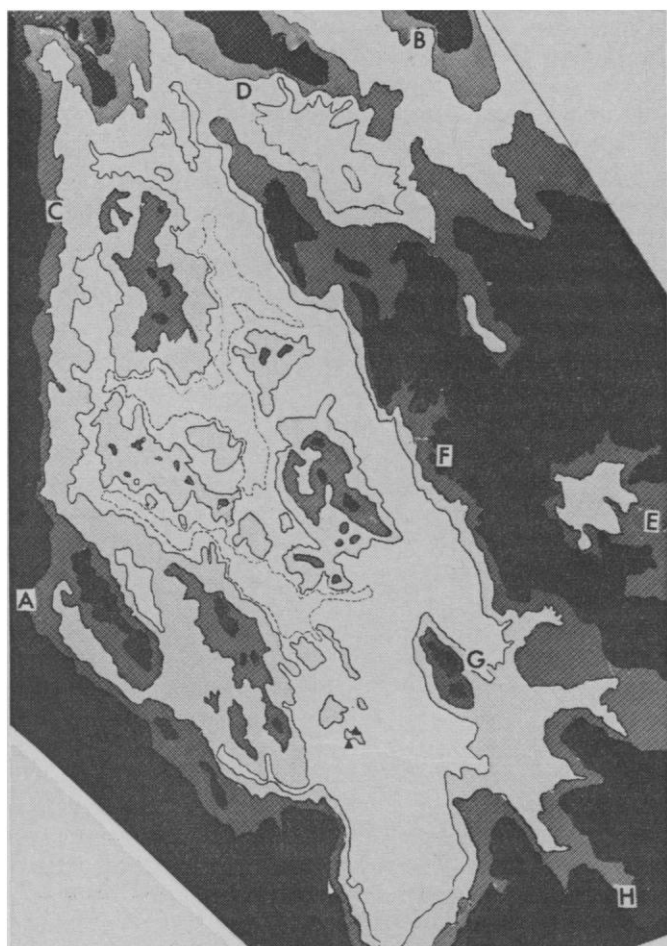


Fig. 5 (left). The Velebit Mountains. Contours at 450 (dotted lines), 500, 600, 700, and 800 meters. Triangles mark positions of temperature recording stations. The letters A to H mark locations for which cross sections are shown in Fig. 7. Fig. 6 (right). Frequency of faint bands (black sector) in *Cepaea vindobonensis* in the Velebit Mountains. The 500-meter contour is shown.

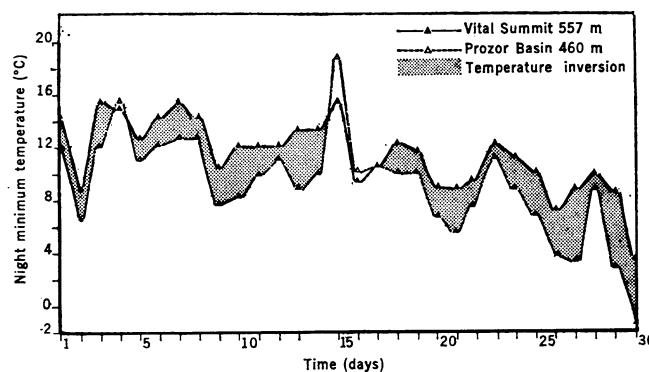
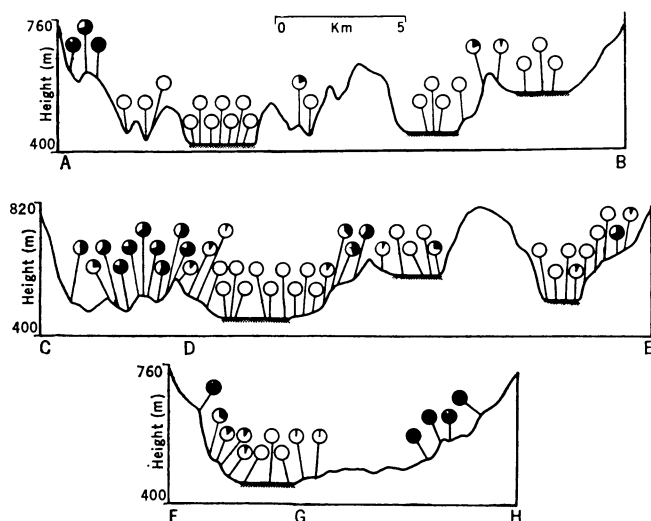


Fig. 7 (left). Sections across the Velebit Mountains (see A to H in Fig. 5) showing association between faint banded shells and topography. Basins are stippled. Fig. 8 (above). Night minimum temperatures at two stations (see triangles, Fig. 5) in the Velebit Mountains from 9 August to 7 September 1971.

are almost absent from the basins themselves. Not all populations living on mountainsides contain faint banded snails, but where this morph does occur it is generally confined to mountain slopes. The association between morph frequency and topography holds true for all seven separate basins in the study area (Fig. 7). None of the other morphs show a convincing association with topography.

Possible Mechanisms of Selection

This simple system of shell polymorphism among populations of *C. vindobonensis* living in a mountainous region reflects a much clearer association of morph frequency with topography than has previously been found in *C. nemoralis*. It may be possible to deduce the nature of the selective agent from a consideration of this association.

Basins such as those in the Velebit Mountains provide ideal conditions for the development of temperature inversions (28). In calm, clear weather, heat is lost by radiation from the earth's surface and cold air flows from the slopes into the basins; these "frost hollows" may therefore become considerably colder than the mountainsides. Night minimum temperatures were measured at the foot and on the summit of a small hill in the center of an extensive basin (Figs. 5, 8, and 9). Temperature inversions developed on 27 of the 30 nights when readings were taken. Over this period the mean minimum temperature was 9.1°C in the basin compared to 11.4°C on the hilltop, 97 meters above the basin floor. Other measurements in this region have shown that temperatures in the basins may be as

much as 17°C below those of the surrounding hillsides (29). Even the differences in mean minimum temperature between stations with a height difference of 100 meters shown in Fig. 8 are comparable to those found between points 700 kilometers apart at sea level in western Europe (30).

Fully pigmented *C. vindobonensis* are commoner in frost hollows than on slopes in the Velebit Mountains. Similarly, dark colored *C. nemoralis* are at a higher frequency in the colder parts of this species' range. It is well known that dark colored animals heat up more rapidly and (in poikilothermic species) attain a higher equilibrium temperature than do light colored individuals in sunlight (31). Desert iguanas, for example, show a 23 percent decrease of heat

input in sunshine when skin color changes from dark to light because of melanophore contraction, and *Colias* butterflies with unpigmented wings absorb only 63 percent as much energy from sunshine as do pigmented individuals. These differences have a considerable effect on the physiology of different colored animals in sunlight. An initially cold and torpid dark colored *Colias* reaches a temperature suitable for activity considerably more rapidly than an unpigmented one when exposed to the sun, as it has a rate of heating approximately 1°C per minute greater than that of the light colored individual. Light colored insects can, however, avoid overheating and remain active for longer periods when placed in bright sunshine on a hot day.



Fig. 9. Inversion mist in the Gacka Basin photographed from the Vital Summit recording station (see Figs. 5 and 8).

Figure 10 shows the relationship between the intensity of band pigmentation and internal temperature for faint banded and fully pigmented snails exposed to the sun. In 13 of 14 similar experiments, fully pigmented snails placed in direct sunshine reached a higher equilibrium temperature than did faint banded individuals of the same size ($\chi^2 = 6.3$; $P < .02$). Sixty-four faint banded and the same number of dark *C. vindobonensis* from a single colony were placed in direct sunshine (sun temperature, 26° to 36°C) after they had been in an inactive state in the shade (temperature, 18°C) for several hours. Water at 18°C was poured onto the snails, and the time to activity (extrusion of the body from the shell) was measured. Fully pigmented snails had a mean time to activity of 20.2 minutes, while that of faint banded snails was 29.9 minutes. This difference is significant (Mann-Whitney U test; $P < .01$).

It is sometimes assumed that dark colored animals will lose more heat by radiative cooling at night. This is not true. The wavelength of radiation from a surface depends on its temperature, which is about 280°K for invertebrates, resulting in a radiation peak of 8 to 10 micrometers. The Kirchhoff law relates the intensity of emission from an object to its absorption of radiation at the same wavelength. A body's absorptivity of visible light (which determines its color) therefore bears no relation to its loss of heat by radiation which has a much longer wavelength. Radiation is in any case much less important than other modes of heat loss in animals (31, 32). There were no significant differences in time to activity of faint banded and fully pigmented *C. vindobonensis* in the shade.

Snails with light colored shells will therefore be favored in situations where they are faced with a severe heat load, while dark shelled individuals will be at an advantage in places where it is necessary to obtain the maximum energy from the sun's rays. There will be no difference in the thermal relations or selective values of differently pigmented snails in the dark. This may help to explain some of the patterns of morph distribution described in this article. Dark banded *C. vindobonensis* shells are found preferentially in frost hollows, and faint banded shells only on steep slopes which have a warmer microclimate because they shed cold air rapidly (28). *Cepaea* is often nocturnal and crepuscular in its activity,

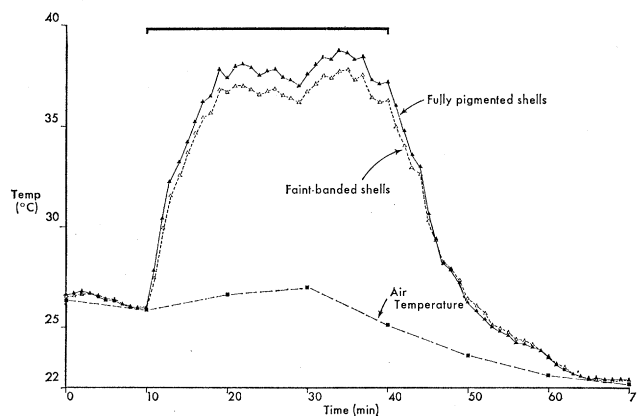


Fig. 10. Internal temperature (measured with a thermistor placed inside the shell) of fully pigmented and faint banded *C. vindobonensis* exposed to sunshine and in the shade. Horizontal bar shows period of exposure to sunshine.

but is active in daylight under cold conditions (33). Snails with fully pigmented bands will warm up more quickly in the early morning sun after a temperature inversion, and this will enable them to reach a temperature suitable for feeding and other activities sooner than faint banded snails. Faint banded snails are at a corresponding advantage in the warmer microclimate of the hillsides. It may be possible to explain some large-scale gene distributions in *C. nemoralis* in similar terms of differential thermal relations with the environment, as the light colored morphs in this species are found preferentially in the warmest parts of its range.

Parkin and I (34) have transferred 7000 marked dark and faint banded *C. vindobonensis* between hillsides and basins in the Velebit Mountains. Future examination of these experimental colonies may provide an estimate of the intensity of microclimatic selection.

Discussion

The investigations of *Cepaea* populations described herein suggest that some geographical variation in gene frequency is greatly affected by climate. It seems unlikely, however, that climatic selection can provide a complete explanation of area effects in *Cepaea*. In many places it has not been possible to associate the frequency of any *C. nemoralis* morph with the environment, and in topographically uniform regions it is in any case unlikely that microclimate could vary sufficiently to exert consistent selective effects. The results that I describe in this article show that some *C. vindobonensis* morph frequencies show no detectable associations with the environment even in the very variable ecology of the Velebit Mountains, and that even populations

of *C. nemoralis* living in very different climates throughout Europe show no consistent trends in the frequencies of the genes controlling the number of shell bands.

The patterns of gene frequency distribution found in *Cepaea* may be explicable in terms of differential integration of the genes controlling shell polymorphism into the genetic background of the population. All four *Cepaea* species show polymorphism for the number of bands on the shell, but only the closely related *C. nemoralis* and *C. hortensis* are polymorphic for shell color, and *C. vindobonensis* for the variation which I have called faint banding. Band number polymorphism is also much more widespread than are other shell polymorphisms throughout the helicid molluscs (35). The genes controlling the number of bands on the shell therefore transcend the limits of the species in the genus *Cepaea*, and perhaps also the limits of the genus itself. Genes which antedate speciation have a long history of evolution in conjunction with many other genes, and may therefore have evolved stronger epistatic interactions with these other loci. Their frequencies may depend more on the strength and direction of such interactions than on direct environmental selection, while those of polymorphic genes with a much more restricted taxonomic distribution may show fewer correlations with other loci and may therefore be more responsive to any selective effects of the environment (36).

The frequencies of genes for shell color in *C. nemoralis* and of those controlling faint banding in *C. vindobonensis* are clearly influenced by environmental selection; it has been possible to identify one selective mechanism from the ecological and behavioral experiments that I have described. Epistatic interactions giving rise to stable

disequilibria involving the genes for shell band number may be more powerful than the interactions at these more recently evolved polymorphic loci. The association of genes controlling band number with gene complexes which are resistant to the disruptive effects of environmental selection may help to explain why it is often relatively difficult to associate their frequencies with an ecological variable.

In other animals, the selective value of gene interactions, the degree of linkage, and the genes involved in the interacting complexes vary from population to population (37). This is also likely to be the case in *Cepaea*, so that the "genetic environment" of the population may often be as important in controlling the distribution of the frequencies of genes for band number as is the ecological environment. In ecologically uniform places even the frequencies of genes such as those controlling *C. nemoralis* shell color may depend primarily on the effects of the genetic background, so that populations develop geographical variations in gene frequency which cannot be related to the environment.

Involvement of such second-order phenomena in the control of population structure means that simple observation of the distribution of individual genes in natural populations is unlikely to provide a complete explanation of the cause of area effects. In spite of this reservation, the results described in this article suggest strongly that climatic selection plays an important part in controlling gene distribution in some mollusc populations.

Summary

Polymorphic snails of the genus *Cepaea* have been widely used for research in ecological genetics. Natural selection by selective predation is important in controlling morph frequencies in some populations of *C. nemoralis* in England. The importance of environmental selection in affecting other patterns of local genetic differentiation of population structure (area effects) is a matter of controversy. Some authors emphasize divergent evolution of whole gene pools between area effects, while others feel that climatic selection acting on individual loci is important.

Analysis of 500,000 *C. nemoralis* snails from throughout Europe shows

that there is a strong positive association between gene frequencies at the shell color locus and mean summer temperature, but that no climatic correlations are obvious at other loci. Another species, *C. vindobonensis*, which has a much simpler system of polymorphism than does *C. nemoralis*, was investigated in Yugoslavia, in a region where there is known to be intense microclimatic differentiation because of the accumulation of cold air in frost hollows. There was a striking tendency for snails with lightly pigmented shell bands to be found in places with a warm microclimate. Physiological and behavioral experiments demonstrate that this is due primarily to differential energy absorption from sunshine by the different shell phenotypes. As in *C. nemoralis*, other *C. vindobonensis* phenotypes show no detectable association with the environment. It is possible that genes whose frequencies cannot be related to environmental selection may have evolved strong linkage interactions with other genes in the population's gene pool. Selection by the ecological environment and the genetic environment may therefore both be important in controlling the genetic structure of snail populations.

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