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Dedicated to Professor Dr. H. Engel

Different phenotypic variation of the snails *Cepaea nemoralis* and *C. hortensis* in a 'mixed' population in Southern Sweden

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ABSTRACT

Attention is drawn to the sympatric occurrence, in a small area in southern Sweden, of a population of *Cepaea hortensis* and one of *C. nemoralis* which show a striking difference in their phenotypic variation. The relative frequencies of the various morphs present in each population are reported. After a discussion of some possible explanations of the different variation patterns, the importance of additional records of such singular "mixed" populations of these species of snails is emphasized.

It has been reported (e.g., Clarke, 1960; also Cain & Wolda, priv. comm.) that phenotypic variation in *Cepaea nemoralis* (L.) and *C. hortensis* (O. F. Müll.) may differ appreciably when these two species of snails occur sympatrically. In how far such reports are of significance depends on a number of circumstances, of which the adequacy of the sampling technique and the uniformity of habitat are the most obvious ones. Assuming that the genetic potential and the genetic constitution of the two species are rather similar, one would expect that longestablished (and hence stabilized) populations occurring in the same biotope exhibit the same pattern of variation if selective pressure affects both species in the same way; in other words, one would expect parallel variation. Therefore, statistically adequate records of phenotypic variation in such 'mixed' populations are of special interest if the variation pattern of the two species is strikingly different.

In July 1967 I discovered such a 'mixed' population living in a restricted area, a patch of woodland near Askim (in the Göteborg area, southern Sweden) very close to a caravan camping site known as 'Båtmanstorpets Campingplats', which adjoins the southern coastal road marked '158'. This locality, 12 to 13 km from the centre of Göteborg City as the crow flies, consists of a small patch of birch forest mixed with some Scotch pine and an occasional young mountain ash, most probably on a granitic subsoil. It is rather isolated by being surrounded by some gardens, grassland, corn fields,

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roads and a hilly rocky outcrop. The undergrowth contains *Juniperus communis, Melampyrum pratense, Veronica officinalis* and some grasses with a few groups of *Aegopodium podagraria* (which last species may be indicative of human disturbance within the forest patch). Near the centre of the forested area there was a rubbish heap mainly consisting of mown-off lawn-grass, cut herbage and partly rotted, discarded bouquets, with some old vegetable crates in various stages of decay and a few lumps of brick and mortar.

After a torrential rain storm, fallen during the previous evening, I visited this waste dump in the early morning and found it teeming with snails, mainly *Cepaea hortensis* and *C. nemoralis*. Although the surface area covered by the rubbish heap was only something like 5 m by 0.75 m, nearly all the specimens gathered in the forest patch and to be discussed presently were taken from this small area and the immediate surroundings, viz., a strip of 0.5 m to 1.0 m alongside. I was immediately struck by the conspicuous difference in the variation pattern of the two species of *Cepaea* present and decided to collect all specimens that were mature enough for a proper identification. The site was revisited during the same day just before dusk and on the two consecutive days in the early morning. The forest surrounding the rubbish heap was also thoroughly combed out and it appeared after a rough estimate of the phenotypic variation and the relative morph frequencies that the variation pattern in an area of about 20 m by 30 m did not differ appreciably from that of the lot taken from the rubbish heap or from very close to it. Presumably the snails, not only attracted by the decaying grass and herbage, rotting wood and lime-containing mortar, but also by the shelter and the moister conditions provided, were habitually accumulating there to feed. Accordingly, the lots taken on or near the dump were certainly representative of the local populations as a whole and it was, therefore, permissible to include the much smaller number of snails taken from the forest around the rubbish heap in the numerical analysis of the morph frequencies.

Apart from the two species of *Cepaea*, the following snails (and some unidentified but common garden slugs) were collected on or near the garbage heap: *Arianta arbustorum* (L.) (rather common), *Bradybaena* (= *Fruticicola*) *fruticum* (O. F. Müll.), the unbanded reddish-brown form only (about 20 recorded), *Trichia hispida* (L.) aggr. (about 10 adult specimens taken, but undoubtedly rather common), and a few *Helicigona lapicida* (L.) (which appeared to be much more common on the surrounding trees and rocks). In addition, in the surrounding forest under stones two specimens of *Oxychilus cellarius* (O. F. Müll.) were found.

The specimens of *Cepaea* were divided in a number of ecologically important colour and pattern classes (which do not necessarily contain only a single morph), as follows:

C. nemoralis, unbanded, coppery red to reddish brown: class "Red-U";
banded 00300, coppery red: class "Red 00300";
banded 00300, yellow: class "Yellow 00300";
banded 12345 (or slight variations such as 12045 and 123(45), reddish yellow: class "R. Yellow 12345"; and

the same banding, but on a yellow background: class "Yellow 12345".

C. hortensis, unbanded, yellow: class "Yellow-U";
unbanded, pale whitish-yellow: class "P. Yellow-U";
hyalozonate (mainly 12345), pale whitish-yellow: class "P. Yellow H.";
banded 12345: class "Yellow 12345".

The contrasting bands are all of the brown type; the mouth lip is always white in the specimens of *C. hortensis* and brown in *C. nemoralis*. The hyaline bands (in *C. hortensis*) are mainly 12345, one was 12045.

The classes are tabulated in table I and a combination of classes as "dark" *versus* "light" is shown in table II.

TABLE I. Numbers of specimens per ecological class and (in brackets) the relative percentages

	Classes								
	Red		*R. Yellow*		*Yellow*			*P. Yellow*	
	U	*00300*	*00300*	*12345*	*U*	*00300*	*12345*	*U*	*H*
C. hortensis	—	—	—	—	196	—	4	5	29
(234 specimens)	(—)	(—)	(—)	(—)	(83.8)	(—)	(1.7)	(2.1)	(12.4)
C. nemoralis	33	1	1	24	—	3	18	—	—
(80 specimens)	(41.2)	(1.3)	(1.3)	(30.0)	(—)	(3.8)	(22.5)	(—)	(—)

TABLE II. Combined results as two groups of morphs, "dark" and "light", respectively

	C. hortensis	*C. nemoralis*
Red and (R.) Yellow 12345 combined ("dark")	4 (1.7%)	76 (95 %)
(R.) Yellow U, or H ("light")	230 (98.3%)	4 (5.0%)

The differences between the two populations are extreme, so much so that Drs. Cain and Wolda told me they did not recollect a comparable case when I discussed the composition of the Swedish population with them. The population being possibly of considerable interest, the collected material, after having been examined by Drs. Cain and Wolda, will eventually be deposited in the Zoological Museum, Amsterdam, with a reference to the present paper.

Switching from the statistical evidence to possible explanations, we must now consider a number of points germane to all population analyses in *Cepaea*, viz., selective pressure, 'area effects' (Cain & Curry, 1963a, b, c; Curry et al. 1964) and factors associated with genetic constitution.

As far as selective pressure by predator selection is concerned, predation by thrushes and by rodents can presumably be ruled out, not only because song thrushes and rabbits are absent or rare in that part of Sweden, but also because such a selection on pattern and on colour or on dark/light contrasts would establish a parallel variation resulting in a more or less equal representation of the various morphs rather than the very different variation pattern actually observed.

As far as the evidence goes, selection by abiotic environmental factors such as effects of the microclimate (solar radiation etc.) need hardly be considered in the rather uniform (shady) habitat, although 'area effects' are of course only manifest in populations occurring in adjacent, different habitats and (if they were present at all) could therefore not be noticed in the case under discussion. The composition of the population of *C. nemoralis* would be perfectly normal in types of mixed forest in many places of Western Europe (e.g., in England, Benelux, northern France, N.W. Germany), especially where thrush predation occurs (Ford, 1964), but the *C. hortensis* population would be definitely incongruous in such an environment. Incongruity being a possible indication of area effects, one might be inclined to accept an area effect, but this would imply that the cause, or causes, of the effect act(s) quite differently on the two species of *Cepaea*, which I consider rather unlikely.

The explanation of the different variation patterns by the possibility of a different genetic composition of the two populations is of course complicated by a number of uncertainties. The two populations need not necessarily both have been long-established and stabilized at a certain level of phenotypic variation. In the early stages of colonization or introduction a number of factors such as primarity of appearance of certain morphs (the first specimens to arrive deciding the initial phenotypic variation according to the 'founder principle' and 'genetic drift') and perhaps also competition with already locally established populations of other species (*Cepaea, Bradybaena, Arianta*) may have different effects. As Dr. Wolda assures me that the corresponding hereditary factors for colour and banding behave rather similarly in the two species of *Cepaea* as far as dominance and linkage are concerned, the dissimilarity of the respective morph frequencies in the two sympatric Swedish populations suggests to me that the one species (*viz. C. nemoralis*) arrived earlier than the other and had time to become stabilized, or, alternatively, that the first specimens of the two species to arrive belonged to phenotypically very different colour and banding classes which were not strongly influenced by subsequent 'visual' predator selection, so that the initial differences were not levelled out.

The number of possibilities being rather large and the possibility of a fortuitous coincidence of circumstances not to be ruled out, the occurrence of such extremely different variation patterns in a single 'mixed' population of *C. hortensis* and *C. nemoralis* need not be more than an exceptional, or an extreme, case and as such hardly of any consequence. If it could be demonstrated, however, that such populations are not infrequent, or even consistently found in similar habits in certain areas (and particularly in southern Sweden), they would be of considerable interest, because certain environmental factors, particularly predation, are lacking or at least insignificant. It is for this reason that the case is here put on record in the hope that our fellow-biologists, in the first place the Scandinavian ones, will be on the look-out for comparable cases in Sweden and elsewhere.

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Dedication

As my old friend, and later also colleague, H. Engel and I share one zoological interest: the study of Mollusca, the inclusion of this paper in a commemoration volume in his honour would seem to fit the occasion admirably.

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