

Climatic selection on body colour in *Cepaea*

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There is geographical variation in body colour in the land snails *Cepaea nemoralis* and *C. hortensis* along a transect of 88 samples from the north of Scotland to the Pyrenees. Paler body colour is associated with higher mean daily maximum temperature in both species. Laboratory experiments show that dark-bodied snails heat up more rapidly and reach a higher equilibrium temperature than do pale snails when exposed to radiant energy. Climatic selection favouring pale body colour in warm areas and dark body colour in cold areas is probably responsible for the association with climate.

INTRODUCTION

Most of the extensive work on the ecological genetics of *Cepaea* land snails has concentrated on the variation in shell colour and banding pattern. These snails also show considerable geographic variation in allozyme frequency, which has been mapped in various parts of Europe (Johnson, 1976; Jones, Selander and Schnell, 1980; Ochman, Jones and Selander, 1983 and in preparation), but which is not correlated with any obvious pattern of selective agents. It is now clear that many evolutionary forces act upon these polymorphisms (e.g., Jones, Leith and Rawlings, 1977).

Students of *Cepaea* have long been aware of a further mode of variation which also shows geographic differentiation: the colour of the soft body of the snails. This variation is at least partially under genetic control (Cain and Sheppard, 1952; Murray, 1963; Cain, Sheppard and King, 1968; Wolda, 1969). Its pattern of distribution has only rarely been considered (e.g., Cain and Currey, 1963) and has never been investigated on a large scale. Here we report a European survey of body colour in *Cepaea nemoralis* and *C. hortensis*; a survey analogous to that for shell characters (Jones, Leith and Rawlings, 1977) which showed that for *C. nemoralis* the proportion of yellow (i.e., pale-coloured) shells in a population is strongly correlated with mean summer temperature. Our transect extends from the north of Scotland to the Pyrenees and also includes samples from Poland

and Denmark. It excludes the most northern populations of *C. hortensis* (in northern Scandinavia) and the most southern populations of *C. nemoralis* (in Spain, Italy and Yugoslavia), but covers the greater part of the climatic ranges of both species.

We describe also some experiments on the thermal relations of dark- and pale-bodied snails.

METHODS

Thirty-five samples of *C. nemoralis* and 53 of *C. hortensis* were collected during 1984; these included samples from five populations containing both species. One sample of *C. nemoralis* came from near Krakow in Poland, and a single mixed-species sample from near Aarhus in Denmark; the remainder came from the U.K. and France (fig. 1). Habitats were classified as follows: habitat type (1) dune and marram grass, (2) cliff-top and cliff-face, (3) short grass, (4) rough herbage (open and unshaded), (5) rough herbage (wood-edge). None of the samples came from within woodlands. The single Polish and Danish sites and one of the Scottish sites (samples 148, 149, 151) were not classified since habitat information was not available. Further details of sampling sites can be obtained from the authors. Whenever possible 50 adult snails were collected at each site, and in the great majority of cases were collected within an area smaller than the panmictic unit for *Cepaea* (approximately 30 m diameter for a

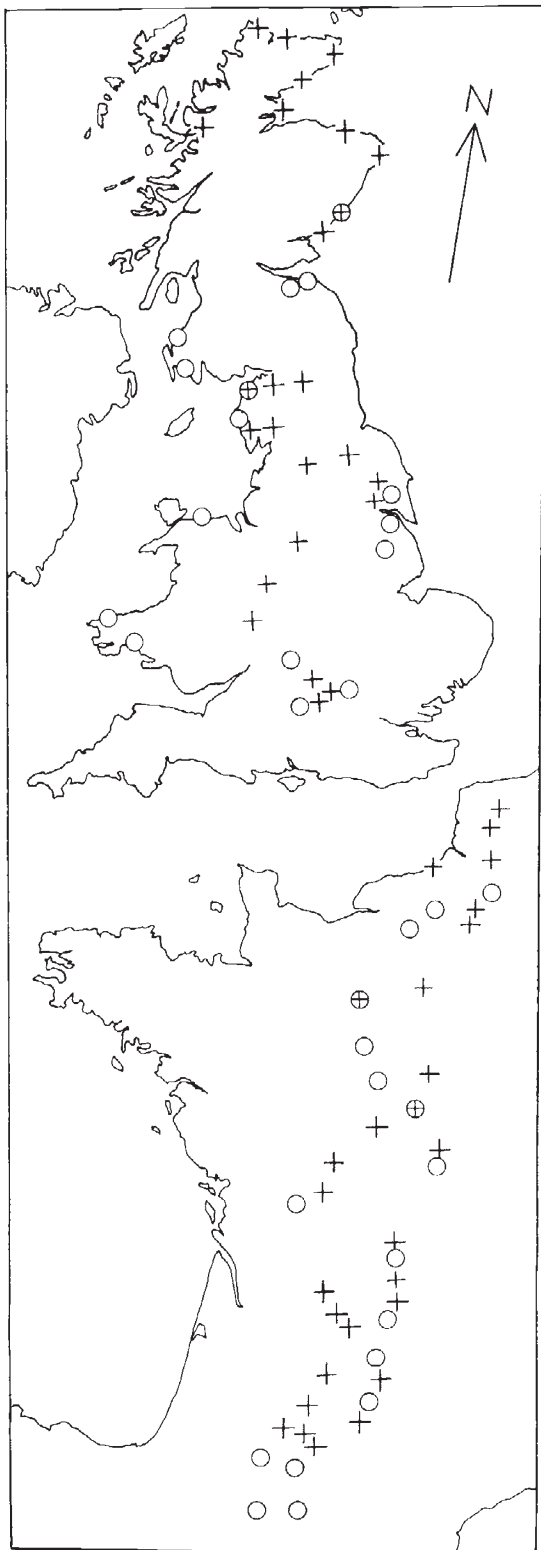


Figure 1 British and French sampling locations. Circles—*C. nemoralis*, crosses—*C. hortensis*, crosses within circles—mixed species samples.

two-dimensional habitat, 50 m for a linear habitat—Lamotte, 1951; Murray, 1962). Mortality meant that the number scored from a sample was sometimes less than 50.

Body colour was scored by matching to the coloured chips in the Munsell Book of Color (1958). Following Cain and Sheppard (1952) and Cain and Currey (1963), the colour was scored on the area between the tentacles of the extended snail. Colour matching was done in an enclosed area under standardised conditions of fluorescent light. There was only slight variation in hue; most snails were greyish, sometimes with a tinge of brown or yellow, and could be scored on pages 10YR, 2.5Y and 5Y of the colour book. This variation in hue has been ignored and body colour matched to the range of 10 neutral shades from black (0) to white (10) to give a measure of darkness or paleness.

Jones, Leith and Rawlings (1977) plotted shell colour against mean daily temperature for July, but we have here used mean daily maximum temperature for July since this is probably of greater importance in snail thermal relations. Temperatures near the sampling locations were obtained from climatic maps of Britain (Meteorological Office, 1975) and France (Météorologie Nationale, 1974) by interpolation between the isotherms on the maps. Temperatures for Krakow and Aarhus were obtained from tables (Meteorological Office, 1967, 1972). Where necessary, the appropriate adjustment of temperature according to altitude was made.

Laboratory experiments were carried out on *C. nemoralis* to test the thermal relations of dark- and pale-bodied snails exposed to radiant heat. The snails used had their shells painted grey to remove thermal differences arising from shell colour and banding, and were drowned immediately before the experiments so that the head and foot were extended out of the shell. They were placed on a polystyrene tile in size-matched pairs of one dark snail (colour score 2, 3 or 4) and one pale snail (colour score 5 or 6). Ten pairs of snails were used. Each pair was illuminated from above by a 150 watt high intensity photo-enlarger light bulb 20 cm above them in a room with an air temperature of 5°C. A sheet of clear plastic was placed between the bulb and the snails to reduce convective heating. The temperatures within the external soft parts were then recorded at one minute intervals using thermocouples inserted into each of the snails' bodies until equilibrium temperatures were reached (*i.e.*, three consecutive readings differed by no more than 0.1°C). Humidity was kept constant during the experiments.

RESULTS

The body colour score of individual snails varied from 2 to 7 in *C. nemoralis*, and from 2 to 8 in *C. hortensis*; a range from dark slate grey to pale creamy-yellow. Mean body colour within samples (tables 1 and 2) ranged from 3.37 to 5.94 for *C. nemoralis* and 2.48 to 6.45 for *C. hortensis*.

Body colour score was regressed on temperature by using all 88 samples without weighting according to sample size (figs. 2 and 3). This was legitimate despite the small size of a few samples since the sampling error associated with the mean scores of body colour was much less than the residual error about the regressions. Those few samples of less than 20 individuals are distinguished in the figures. The linear regression for *C. nemoralis* is:

$$\text{body colour score} = 1.67 + 0.13 T$$

and for *C. hortensis* is:

$$\text{body colour score} = 0.98 + 0.14 T$$

in which T represents mean daily maximum July temperature in °C. The slopes of these regressions are significantly different from zero ($p < 0.001$ for both species), and the 95 per cent confidence limits of the regression coefficients indicate no significant difference between species in either slope or intercept (*C. nemoralis*— 1.67 ± 1.71 and 0.13 ± 0.08 ; *C. hortensis*— 0.98 ± 1.08 and 0.14 ± 0.05). There is therefore a strong tendency in both species for populations living in relatively warm places to have high frequencies of animals with pale bodies.

Most samples were taken from rough herbage (nettles, brambles, etc.) in roadside verges or ditches bordering fields; a few were taken from dunes, cliffs and open areas of short grass; but only a small number came from rough herbage at edges of woodland, and none from woodland (tables 1 and 2). Thus, our samples come from a fairly uniform set of open habitat populations, and it is not surprising that there is little relation of body colour to habitat type (figs. 2 and 3). The only hint of such an association is in *C. hortensis*, in which populations from dunes, cliffs and short grass tend to lie above the regression line of colour on temperature (fig. 3). This is not shown by *C. nemoralis*.

In all 10 laboratory experiments the dark snail heated up more quickly and reached a higher equilibrium temperature than the pale snail. The difference in equilibrium reached ranged from 0.13 to 1.27°C (table 3). The mean difference was 0.57°C. Fig. 4 shows the results of a typical experiment in which the difference in equilibrium reached was approximately 0.5°C. The variation

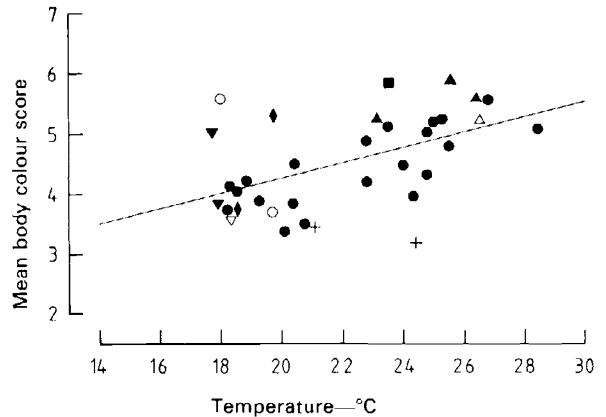


Figure 2 Regression of population mean body colour score on mean daily maximum July temperature (T) for samples of *C. nemoralis*. Samples are symbolised according to habitat type (see text): habitat type 1—diamonds, 2—downward-pointing triangles, 3—squares, 4—circles and 5—upward-pointing triangles. Open symbols represent samples of less than 20. Crosses represent samples not classified according to habitat (both of less than 20). Sites classified as intermediate between types 4 and 5 (4/5 in tables 1 and 2) are symbolised as type 5.

between these results is due partly to the greater or lesser contrast in colour between the snails used in each experiment, and to the difficulty of inserting the thermocouples in exactly the same position in each snail.

DISCUSSION

Cain and Sheppard (1952) argued that for their southern English populations of *C. nemoralis* differential visual selection by predators in open and woodland habitats was the underlying cause of geographical variation in body colour. By taking most of our samples from open habitats we have reduced the amount of variation along our transect which is explicable by visual selection and our samples are therefore not appropriate for testing this claim. Cain and Currey (1963) pointed out that Cain and Sheppard's results might also be explained, at least partially by climatic selection since insolation is greater in open habitats and pale-bodied snails may be favoured there for this reason also. The slight hint that *C. hortensis* from dunes, cliffs and short grass tend to be paler agrees with either hypothesis.

We have found extensive large-scale geographic structuring for body colour variation in Europe. This is strongly related to temperature, and is probably determined at least in part by

Table 1 Mean and variance of body colour score, with sample size (*n*), habitat type (see text) and grid reference (National Grid for U.K.; Lambert zones I, II and III for France) for populations of *Cepaea nemoralis*

Sample	<i>n</i>	Mean	Variance	Habitat type	Grid reference
Britain					
27	5	5.600	0.300	4	NO 775 658
40	51	4.098	0.570	4	NY 026 024
41	60	4.083	0.925	4	NY 020 336
43	25	5.000	0.833	2	NX 092 863
44	40	3.725	0.461	4	NX 202 542
46	45	3.889	1.237	4	SE 874 602
47	49	3.367	0.946	4	TA 063 088
48	55	3.855	0.682	4	TF 128 792
49	38	4.526	0.851	4	SU 345 848
50	32	3.813	1.125	2	SM 892 413
51	51	5.294	0.732	1	SN 326 082
52	14	3.714	0.527	4	SP 123 333
146	24	3.500	0.696	4	SP 924 176
147	45	4.222	0.949	4	NT 270 691
150	35	3.743	0.608	1	NT 449 788
152	9	3.667	1.000	2	SH 781 836
France					
102	41	4.195	0.761	4	5932 2382 I
108	51	5.216	0.613	4	5608 2795 II
111	50	4.820	0.396	4	5715 2076 II
113	25	4.480	0.593	4	5545 0813 II
116	8	5.250	0.500	4/5	5312 3102 III
117	37	5.595	0.581	4	5383 2660 III
119	45	5.089	0.492	4	5315 2170 III
122	47	5.936	0.322	4/5	4701 1280 III
123	40	5.275	0.819	4	4725 0898 III
124	43	5.884	0.772	3	4184 0706 III
125	49	5.612	0.742	4/5	4179 1561 III
134	37	5.054	0.996	4	3978 1279 II
138	47	4.319	0.961	4	4940 3008 II
139	40	3.975	0.692	4	4822 3316 II
140	43	5.140	0.885	4	4690 0980 I
141	42	5.286	0.746	5	5105 1819 I
142	51	4.902	0.730	4	5345 2172 I
Poland					
148	5	3.200	0.200	—	—
Denmark					
149	9	3.444	1.778	—	—

climatic selection acting to favour paler body colour in areas of higher temperature. Our experiments show that the thermal properties of differently coloured snails accord with this explanation, which is similar to that used by Cowie (1983) to explain variation in the colour of the soft parts of the snail *Theba pisana* over a large part of its range. Climatic selection on body colour may hence be analogous to that acting on shell colour (Jones, Leith and Rawlings, 1977) which favours paler shells in hotter areas because of their greater reflectivity of incident solar radiation, and darker shells

in cooler places because of their greater ability to absorb radiation (Jones, 1973; Heath, 1975).

The wide scatter of points about the regressions (figs. 2 and 3) may arise from variation in other selective agents not related to the overall climatic trend, such as visual selection by predators (although variation in this has been reduced by our sampling method—see above), and perhaps because of random processes; also, the temperatures used for the regressions took no account of any microclimatic variations in thermal regime which might exist.

Table 2 Mean and variance of body colour score, with sample size (*n*), habitat type (see text) and grid reference (National Grid for U.K.; Lambert zones I, II and III for France) for populations of *Cepaea hortensis*

Sample	<i>n</i>	Mean	Variance	Habitat type	Grid reference
Britain					
9	46	4.152	0.396	4	SU 415 850
12	44	3.705	1.907	4/5	SU 785 986
13	41	3.439	0.302	4	SP 447 102
14	46	3.935	0.373	5	SD 897 640
15	45	3.333	0.272	4	SK 150 827
16	28	3.107	0.099	4	SJ 736 173
18	24	3.208	0.433	4	SO 612 689
20	28	2.750	0.269	4	SD 116 937
21	20	3.450	0.366	3	SD 486 925
22	8	3.000	0.571	4	NY 323 492
23	32	3.594	0.636	4	NY 684 512
24	25	2.480	0.260	4	SE 255 952
25	20	3.550	0.997	4	SE 953 426
27	6	3.333	0.267	4	NO 775 658
28	50	3.200	0.653	2	NK 094 355
30	28	2.500	0.333	4	NJ 663 653
31	39	4.179	0.467	1	NH 872 767
32	51	3.843	0.455	2	ND 033 152
33	15	3.867	0.410	1	ND 343 556
34	39	4.590	0.511	4	NC 714 625
35	22	4.318	0.417	3	NC 393 687
37	29	2.586	0.323	4	NG 865 346
43	50	3.700	0.500	2	NX 092 863
45	47	3.851	0.477	4	SE 863 663
151	7	4.571	0.286	—	NO 682 443
France					
101	45	3.867	0.482	4	5970 3131 I
103	34	3.912	0.750	5	5900 2325 I
104	30	4.900	0.714	4	5745 2061 I
105	39	4.128	0.904	4	5283 1221 I
107	45	4.511	0.528	5	5568 3130 II
108	46	5.283	0.341	4	5608 2795 II
110	32	5.156	0.846	4	5722 2156 II
112	42	4.452	0.888	4	5555 0891 II
114	32	4.813	1.125	4/5	5579 3599 III
115	36	4.028	0.371	4	5526 3267 III
118	50	5.060	0.466	5	5386 2443 III
120	50	6.000	0.980	5	5251 1878 III
121	34	5.000	0.848	4	4839 1599 III
126	40	6.450	0.613	4/5	4279 1857 III
127	39	6.154	1.397	4	4553 1843 III
128	51	5.647	1.273	4/5	4521 2125 III
129	40	3.275	0.256	4/5	4698 2417 III
130	39	4.256	1.459	4	4950 2946 III
131	44	4.364	0.795	4	4802 3161 III
132	51	4.588	1.127	5	4597 3316 III
135	39	5.051	0.786	4/5	4345 1469 II
136	48	4.625	0.750	4	4637 1906 II
137	38	4.395	0.732	4/5	5005 2456 II
140	45	4.711	0.619	4	4690 0980 I
143	48	3.979	0.617	4	5342 2503 I
144	52	5.077	0.386	4	5740 2846 I
145	50	3.640	0.317	4/5	5753 3069 I
Denmark					
149	12	3.167	1.242	—	—

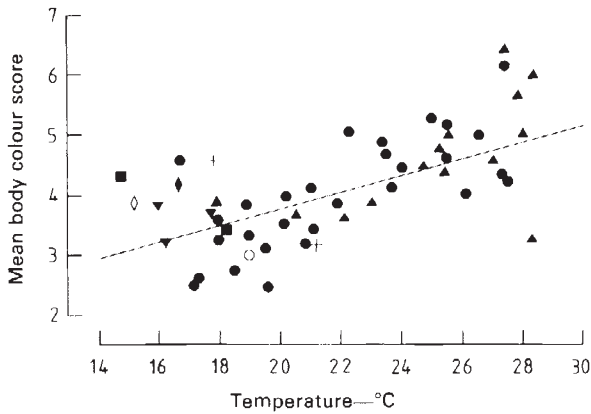


Figure 3 Regression of population mean body colour score on mean daily maximum July temperature (T) for samples of *C. hortensis*. Symbolisation as in fig. 2. Samples not classified according to habitat type (crosses) were again of less than 20.

The mechanism of action of climatic selection on body colour is not known. High temperatures could kill dark-bodied snails (as appears to be the case for dark-shelled individuals—Richardson, 1974), and low temperatures may prevent adequate activity, feeding and growth of pale-shelled snails. Climatic selection might also act on other components of fitness such as fecundity, mating ability or developmental time.

Since snails are very vulnerable to overheating and desiccation when active, to an extent much greater than when resting and withdrawn inside their shells (Riddle, 1983), it is possible that the importance of climatic selection is greater for body colour than for shell colour and pattern. Thus body colour might show a closer relation with temperature than does shell phenotype, and the latter might be more influenced by local variations in visual selection and other factors. This might

Table 3 Equilibrium temperatures (°C) reached (mean of last three readings) by dark and pale snails in the 10 laboratory experiments

Dark	Pale	Difference
13.63	13.07	0.56
15.57	15.03	0.54
11.63	10.77	0.86
14.37	13.67	0.70
15.37	14.63	0.74
15.03	14.73	0.30
14.77	14.07	0.17
13.70	13.57	0.13
15.40	14.13	1.27
14.33	13.87	0.46

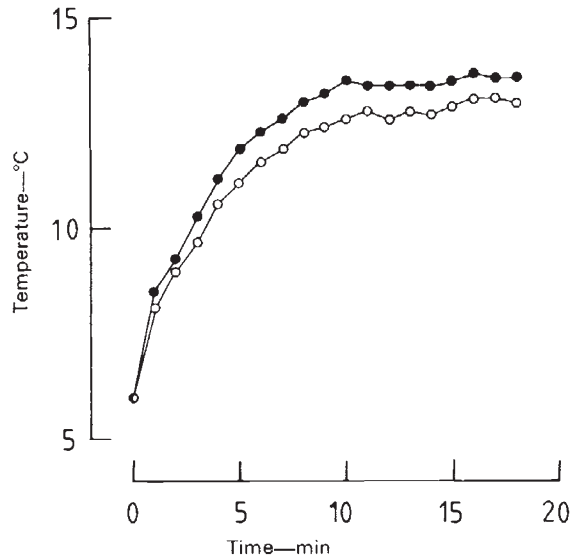


Figure 4 Body temperatures of a dark snail (solid circles) and a pale snail (open circles) exposed to the radiant light source.

explain the strength of this association between body colour and temperature, despite the relatively small numbers of samples available. In addition, Lewontin (1984) has shown theoretically that it is intrinsically more difficult to detect population differences in characters controlled at a single locus than in polygenic characters, so we would also expect trends in body colour to be more easily demonstrable than trends in the frequencies of the shell colour and pattern alleles. For this reason we have not considered large-scale geographical trends in shell colour and pattern in these samples. Such trends can only safely be interpreted if very large numbers of large samples are available (e.g., Jones, Leith and Rawlings, 1977).

This study adds to our knowledge of the ecology and evolution of thermal relations in animals, knowledge largely derived from studies of insects (e.g., reviews in Heinrich, 1981) and lizards (e.g., reviews in Gans and Pough, 1982). Body colour is well known to influence internal temperatures of small poikilotherms (e.g., Watt, 1968). It can of course also be important for camouflage, as a warning signal, for use in courtship and in species recognition. Variation in body colour in some terrestrial slugs (*Arion* spp.) has been suggested to be aposematic (Scharff, 1891), and dark body colour in the land snail *Arianta arbustorum* at high altitudes explained not only in terms of ability to warm up at low temperatures but also as a shield from ultra-violet radiation

(Burla and Stahel, 1983). Here we have demonstrated that climatic selection influences body colour in both *C. nemoralis* and *C. hortensis*. However, there is little doubt that many other agents are operating on this system of variation and that the importance of these will differ among localities. The control of body colour in *Cepaea* may well be a problem with just as many solutions as is the control of the shell polymorphism.

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