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SHELL SIZE AND THICKNESS IN ADULT *CEPAEA NEMORALIS* (L.) (GASTROPODA) FROM THE BELGIAN COASTAL DUNES

by

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1. Introduction

Natural populations of *Cepaea* show a remarkable polymorphism in colour and banding pattern of the shell, that has been the concern of many authors. Little attention has been paid to variations in shell dimensions, which are in part inherited and a useful subject for ecological genetic study (Cook, 1967 ; Cook & O'Donald, 1971 ; Wolda, 1969). In this paper we describe a geographic trend in the mean size, shape and thickness of shell for populations of *Cepaea nemoralis* (L.) from the belgian coastal dune area.

2. Materials and methods

The samples used for shell measurement and weight determination came from collections previously studied for shell colour and banding polymorphism (De Smet, 1982). The samples cover the whole belgian coastal dune region (about 65 km length), extending from the most southern part (Westhoek) to the most northern part (Zwin). Four habitats were collected : *Ammophila*, herbage, scrub and *Rubus*. Adult shells (with lip to shell aperture) only were used ; no distinction was made between age classes.

Height, breadth and spire index were taken to measure shell size and shape. The height was taken parallel to the columella and the breadth perpendicular to the height (fig. 1) ; the spire index is the ratio of height to breadth.

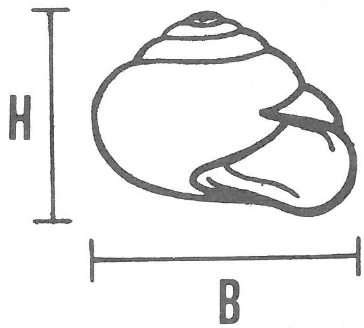

FIG. 1. – Measurements used in this study : height = H ; breadth = B.

Empty air-dried shells were weighed to 0.1 mg. The shell thickness index, viz., the square root of shell weight divided by shell length times breadth (POLLARD, 1975) was taken as an indirect measure of shell thickness.

The larger samples were tested by a one way analysis of variance, for variation in shell dimensions with banding and colour.

3. RESULTS

Table 1 gives the habitat, the sample size, and the means for height, breadth, spire index, weight and thickness index of each population sampled.

3.1. *Shell size*

The mean shell breadth of the populations varies from 19.49 ± 0.87 mm (Blankenberge 44) to 21.66 ± 1.01 mm (Westhoek 1) ; the mean shell height varies from 16.25 ± 0.79 mm (Blankenberge 44) to 18.0 ± 0.94 mm (Het Zoute 49). The spire index ranges from 0.783 (Westhoek 1) to 0.862 (Bredene 37 and De Haan 41). The adult shell width reported for western european populations is 19-32 mm, the most common breadth being 20-22 mm (e.g. ADAM, 1960 ; CAMERON, 1969 ; COOK & O'DONALD, 1971 ; COOK & PEAKE : 1960, 1962 ; LAMOTTE, 1951 ; SACCHI & VALLI, 1975 ; WOLDA, 1969 ; etc.).

To test whether there are trends in shell dimensions with colour and banding, the different morphs within each colony were subjected to a one way analysis of variance. Significant differences do occur, but not in all

Table 1

Mean height, breadth, weight, spire index (S.I.) and thickness index (T.I.) for shells of Cepaea nemoralis *from the belgian coastal dune region*

Locality	Habitat	N	Height ± s (mm)		Breadth ± s (mm)		S.I.	N	Weight ± s (mm)		T.I.
1. Westhoek	A	108	16.88	0.75	21.55	0.71	0.783	77	631.3	164.8	6.91
2. Westhoek	S	80	17.44	0.90	21.66	1.01	0.805	75	709.7	153.5	7.05
3. De Panne	S	14	17.54	1.06	21.33	0.89	0.822	14	799.2	222.0	7.56
5. Koksijde	H	65	17.08	0.93	20.89	0.90	0.818	64	716.6	188.5	7.50
6. Koksijde	S	54	16.87	0.90	20.72	1.06	0.814	54	683.5	184.1	7.48
7. Koksijde	S	24	16.59	0.71	21.09	0.92	0.787	24	754.6	189.3	7.85
8. Koksijde	A	67	16.90	0.71	21.04	0.91	0.803	67	786.8	187.3	7.89
9. Koksijde	S	138	16.67	0.73	21.04	0.81	0.792	138	790.1	152.7	8.01
10. Koksijde	S	193	16.82	0.90	21.08	0.96	0.798	188	756.2	155.6	7.76
11. Oostduinkerke	H	121	16.74	0.73	21.04	0.85	0.796	121	686.3	110.3	7.44
12. Oostduinkerke	H	108	16.92	0.83	21.13	0.99	0.801	107	711.1	151.2	7.46
13. Oostduinkerke	S	56	16.39	0.86	20.68	0.82	0.793	54	751.2	185.0	8.09
14. Oostduinkerke	S	76	17.11	1.02	21.18	0.96	0.808	76	738.4	199.6	7.50
15. Nieuwpoort	S	58	17.30	0.79	21.45	0.99	0.807	58	933.9	197.5	8.23
16. Nieuwpoort	A	135	16.91	0.83	20.96	0.91	0.807	130	820.8	162.9	8.08
17. Nieuwpoort	R	139	16.76	0.75	20.72	0.96	0.809	113	755.6	132.7	7.92
18. Nieuwpoort	H	146	17.57	0.80	21.17	0.87	0.830	146	978.7	167.4	8.41
19. Nieuwpoort	R	19	17.25	1.05	21.61	1.23	0.798	19	781.9	144.7	7.50
20. Nieuwpoort	R	90	16.81	0.76	20.55	0.74	0.818	90	942.5	221.6	8.89
21. Nieuwpoort	A	12	17.18	0.75	21.23	0.60	0.809	20	868.4	212.3	8.08
22. Lombardsijde	S	100	16.94	0.80	21.22	1.01	0.798	75	721.1	188.4	7.47
23. Lombardsijde	S	61	16.56	0.77	20.76	0.93	0.798	60	759.0	218.1	8.01
24. Westende	A	59	16.51	0.69	20.65	0.97	0.800	58	721.9	197.5	7.83
25. Westende	S	12	16.28	0.71	20.44	0.66	0.796	12	713.3	167.9	8.03
26. Westende	S	35	16.85	0.80	21.32	0.84	0.790	34	745.7	198.1	7.60
27. Westende	S	44	16.96	0.68	21.01	0.87	0.807	44	668.6	154.3	7.26
28. Westende	S	27	16.32	0.81	20.55	0.96	0.794	25	671.2	183.9	7.72
29. Westende	A	22	16.76	0.75	20.88	0.88	0.803	19	772.8	156.5	7.94
30. Middelkerke	A	122	16.72	0.86	20.98	0.91	0.797	63	602.0	103.1	6.99
31. Middelkerke	S	27	16.35	0.82	20.62	0.97	0.793	25	754.8	210.0	8.15
32. Ravesijde	A	101	16.83	0.85	20.77	1.06	0.810	62	739.5	156.1	7.78
33. Oostende	A	5	16.64	0.63	20.60	0.69	0.808	6	559.7	145.5	6.90
34. Oostende	A	74	16.79	0.74	20.39	0.95	0.823	73	680.4	125.7	7.62
35. Bredene	H	13	16.87	0.73	20.77	1.07	0.812	13	690.5	144.0	7.50
36. Bredene	A	14	17.04	0.94	20.75	0.92	0.821	13	687.9	169.7	7.42
37. Bredene	S	10	17.50	1.25	20.30	0.66	0.862	10	595.6	138.1	6.87
38. De Haan	H	37	17.03	0.82	20.34	0.74	0.837	36	653.8	172.9	7.38
39. De Haan	S	29	16.93	0.98	20.64	0.84	0.820	29	604.1	176.1	7.03
40. De Haan	R	71	17.28	0.74	20.52	0.78	0.842	70	626.3	92.5	7.06
41. De Haan	H	185	17.63	0.76	20.46	0.84	0.862	124	658.5	120.4	7.11
42. Wenduine	S	21	16.61	0.92	20.73	1.24	0.801	20	661.0	211.7	7.47
43. Wenduine	A	17	17.12	0.68	20.70	0.96	0.827	17	660.4	216.1	7.25
44. Blankenberge	H	149	16.25	0.79	19.49	0.87	0.834	148	608.5	146.4	7.79
45. Blankenberge	A	35	16.37	0.81	20.27	0.98	0.808	35	637.2	175.2	7.61
48. Het Zoute	S	9	17.68	0.69	21.49	0.99	0.823	7	775.5	175.2	7.33
49. Het Zoute	A	14	18.00	0.94	21.18	1.04	0.850	14	745.5	165.2	7.15
50. Zwin	A	192	17.94	1.15	21.28	1.12	0.843	132	824.8	176.2	7.52

A : *Ammophila* ; H : herbage ; S : scrub ; R : *Rubus*.

populations, nor are the directions of the size differences always the same. Of the 47 colonies, 17 showed a significant difference in shell size with colour and/or banding ; these colonies and the directions of the differences are given in table 2.

For both height or breadth, most of the significant size differences concern the colour class ; only a few colonies show a significant difference between banding class. In the colour class there is a tendency for yellow shells to have a larger mean height and/or mean breadth as the pink ones. The situation for the banding class is less clear. However, it does seem that the dimensions of the five-banded shells are more likely to be on the larger size (height or breadth) south-west from Oostende (locality 34) and on the smaller size north-east from that locality.

Table 2

Analysis of variance of the shell height and breadth of C. nemoralis, *and direction of differences with colour and banding*

			Height			Breadth		
Locality	Component	d.f.	F	p	Direction	F	p	Direction
5. Koksijde	Colour	1,59	0.66	n.s.	–	5.51	< 0.025	Y > P
6. Koksijde	Banding	1,50	0.45	n.s.	–	5.19	< 0.05	5 > 0
11. Oostduinkerke	Colour	1,115	0.38	n.s.	–	6.82	< 0.025	Y > P
	Banding	2,115	2.28	n.s.	–	3.16	< 0.05	5 > 0 > 10345
13. Oostduinkerke	Colour	2,50	3.23	< 0.05	Y = P > B	1.91	n.s.	–
15. Nieuwpoort	Colour	2,53	3.26	< 0.05	Y > P > B	3.20	< 0.05	P > Y > B
	Banding	2,53	3.56	< 0.05	3 > 5 > 0	2.47	n.s.	–
17. Nieuwpoort	Colour	2,133	2.05	n.s.	–	4.82	< 0.01	B > Y = P
	Banding	3,133	2.26	n.s.	–	3.26	< 0.025	0 > 5 > 3 > 10345
18. Nieuwpoort	Colour	2,138	3.27	< 0.05	B > P > Y	0.66	n.s.	–
20. Nieuwpoort	Colour	1,86	4.36	< 0.05	Y > P	0.01	n.s.	–
22. Lombardsijde	Colour	1,96	0.74	n.s.	–	5.48	< 0.025	Y > P
24. Westende	Banding	2,53	3.69	< 0.05	5 > 3 > 0	2.35	n.s.	–
34. Oostende	Colour	1,68	15.02	< 0.01	Y > P	3.77	< 0.05	Y > P
38. De Haan	Banding	1,33	6.28	< 0.01	3 > 5	1.41	n.s.	–
39. De Haan	Colour	1,25	8.05	< 0.01	Y > P	3.04	n.s.	–
40. De Haan	Banding	1,66	6.56	< 0.025	3 > 5	0.01	n.s.	–
41. De Haan	Colour	1,180	5.85	< 0.025	Y > P	0.83	n.s.	–
	Banding	2,180	9.26	< 0.01	0 > 3 > 5	5.33	< 0.01	0 > 3 > 5
45. Blankenberge	Colour	1,31	0.79	n.s.	–	6.50	< 0.025	P > Y
50. Zwin	Colour	1,186	0.00	n.s.	–	5.37	< 0.025	Y > P

d.f. = degrees of freedom ; F = variance ratio ; p = probability value.
Y = yellow ; P = pink ; B = brown ; 0 = 00000 ; 3 = 00300 ; 5 = 12345.

The relationships of the shell dimensions with distance north-east across the dune area were studied ; the significance of these relationships has been tested by the Spearman's rank correlation test. Shell height shows no significant relationship ($r_s = 0.087$) and remains more or less constant over the whole area, whereas shell breadth decreases significantly ($r_s = -0.476$, $p < 0.001$) with increasing distance north-east. It follows that variations in spire index are largely determined by shell breadth. In fig. 2 the spire index is plotted against distance NE, and shows a significant increase ($r_s = 0.547$, $p < 0.001$) with increasing distance NE, thus giving shells from more northern populations a more highly spired appearance.

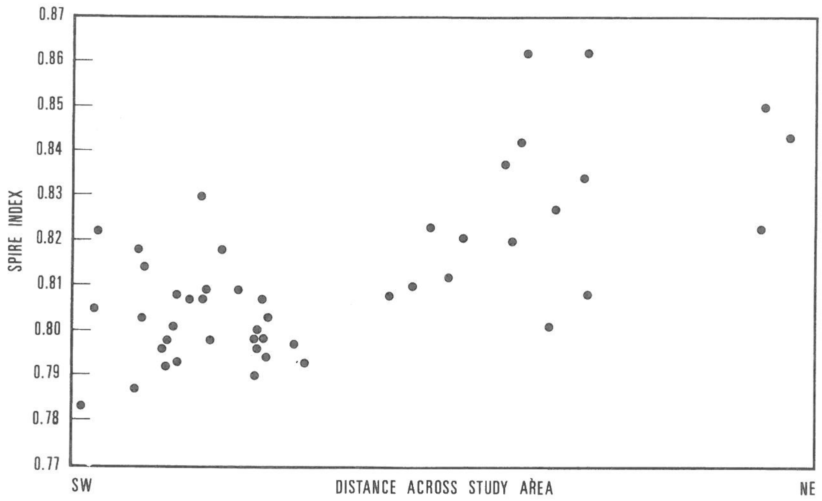

FIG. 2. – Distribution of spire index along the south-west - north-east transect.

3.2. *Shell thickness*

Shell weight determinations were performed in spite of the fact that it is not always possible to remove all the sand from a shell collected on the dunes, and the evidence for age dependent weight differences (WILLIAMSON, 1976). This may in part explain the high standard deviations, although weight differences of ± 20-30 % were found to be normal for shells of old adult snails collected in the first week of may 1981, and weighed after killing and carefully removing the bodies, followed by air-drying at room temperature for several months.

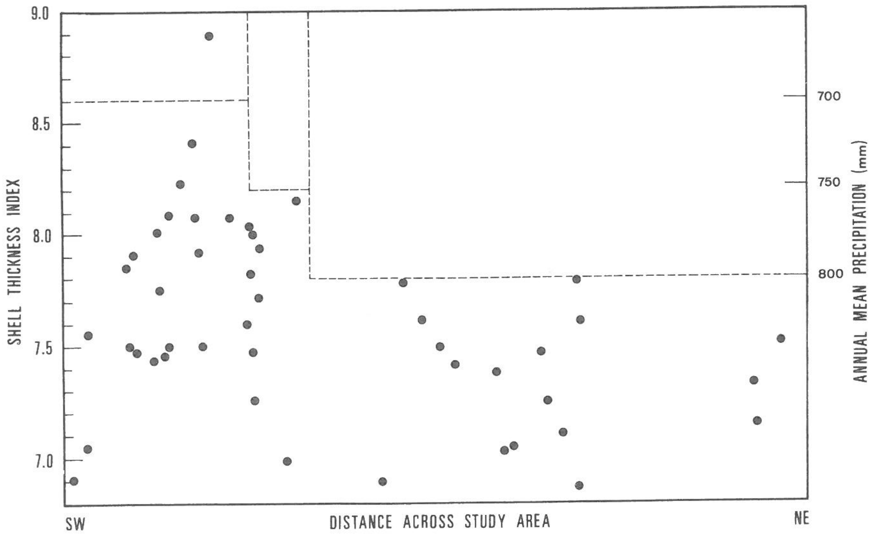

FIG. 3. –Distribution of shell thickness index along the south-west - north-east transect.

Mean shell weight of the populations sampled varies from 559.7 ± 145.5 mg (Oostende) to 978.7 ± 167.4 mg (Nieuwpoort 18) ; their shell thickness index varies between 6.87 (Bredene 37) and 8.89 (Nieuwpoort 20). Both weight ($r_s = -0.392$, $p < 0.008$) and thickness index ($r_s = -0.307$, $p < 0.038$) show a significantly decreasing trend with increasing distance north-east (fig. 3).

3.3. *Shell characters and climate*

Shell characters were compared to habitat, relative population size and climate. Climate only showed a correlation with shell size and weight.

The climate classification by the Thornthwaite method (DINGENS & VERNEMMEN, 1963) based on the water balance, reveals a climatic gradient among a SW-NE transect in the dune area. This climatic gradient is characterized by an increasing humidity, determined by increases north-east in precipitation, water surplus and run off, and decreases north-east in actual evapotranspiration, accumulated potential water loss, water deficit and aridity index. Comparison of shell characters with climate shows that *Cepaea nemoralis* reaches smaller shell breadth and larger spire index, and small shell weight and thickness index in the more humid stretch of the dune area. Table 3 summarizes the mean values of shell characters for mean annual precipitation.

Table 3

Mean shell characters and annual precipitation

Precipitation (mm)	700	750	800
Colony N°	1-21	22-31	32-47
Height[a] (mm)	16.95 ± 0.87	16.70 ± 0.81	17.17 ± 1.06
Breadth[a] (mm)	21.07 ± 0.94	20.93 ± 0.96	20.54 ± 1.10
Spire index[a]	0.805 ± 0.012	0.797 ± 0.005	0.828 ± 0.019
Weight[b] (mg)	782.77 ± 191.60	704.97 ± 186.60	680.90 ± 167.76
Thickness index[b]	7.78 ± 0.46	7.70 ± 0.37	7.34 ± 0.29
[a]Number	1703	509	976
[b]Number	1635	415	809

4. Discussion

The variation in shell size is known to be under polygenic control (Cook, 1967 ; Wolda, 1969) with a heritability of about 60% in *C. nemoralis* (Cook, 1967) and about 70% in the related *Arianta arbustorum* (Cook, 1965). Shell thickness is reported to be under genetic control for *Helix pomatia* (Pollard, 1975). By the high heritability any selection operating on the shell dimensions may be directional or stabilizing. Stabilizing selection acting upon size of *A. arbustorum* by eliminating the aberrant shaped individuals was shown by Di Cesnola (1907). Cook & O'Donald (1971) have studied the variation in survival with size in over-wintering *C. nemoralis*, and found that under experimental mild winter conditions there is strong selection favouring large sized individuals from some colonies. They also found evidence for colour and banding genes affecting adult size. Shell breadth and both oviposition frequency and clutch size were found to be positively correlated (Wolda, 1967). Output differences of some 15% might be the result of breadth differences as small as 1 mm between one snail and another (Wolda, 1963). A large adult size is associated with a faster growth rate in juveniles (Wolda, 1969). It is clear that small differences in size may be responsible for remarkable differences in survival, growth and output.

The data for *C. nemoralis* from the belgian coastal dune area show that mean size, shape and thickness of the shells are less different for the different populations. However, there exists a conspicuous geographic trend for size and thickness, associated with a climatic gradient. WILLIAMSON *et al.* (1976) and TATTERSFIELD (1981) found that shell size may be negatively correlated with population density. As we could not demonstrate any relationship between both size and thickness, and relative population density, the geographic trend in shell variation is presumed to be the result of climatic selection. The snails living on the more humid stretch of the dune area show a reduction in shell breadth and shell thickness. This implies that a more harsh climate favours small size and thin shells, and a warmer and arid climate large size and thick shells. RENSCH (1932) comparing two Italian populations with two German populations of *C. nemoralis* found that the higher dimensions of the first were determined by a higher rainfall. He also found that a lot of species, but not *Cepaea*, have thicker shells under intensive solar radiation and during drier summer periods. POLLARD (1975) found thicker shells of *Helix pomatia* to be associated with areas of low rainfall. The variations in size and thickness we observed point towards a selective pressure by climate. The directions of these variations agree with what might be expected if thickness and body size themselves have an adaptive value. In the more arid environments the amount of evaporation will be less for a thick, and large shell having a more favourable surface area/volume ratio.

SUMMARY

Shell size and thickness of adult *Cepaea nemoralis* (L.) was studied in the belgian coastal dune area. Larger and thicker shells are associated with the most arid stretch ; the area with high precipitation shows smaller and thinner shells. Colour and banding genes may affect adult size.

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