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DIFFERENTIAL HEAT DEATH OF *CEPAEA NEMORALIS* (L.) (GASTROPODA) ON THE BELGIAN COASTAL DUNES

by

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SUMMARY. – The morph frequencies of dead-intact shells of *Cepaea nemoralis* from the Belgian coastal dune area were compared with the live snail populations.

Pink, five-banded pink, five-banded shells in general, and shells with band-fusions are over-represented in dead-intact shell collections.

Yellow, brown, yellow unbanded, and midbanded shells in general, are under-represented in the dead-intact shell collections.

The results are discussed in the light of selective heat mortality.

1. INTRODUCTION

The helicid snail *Cepaea nemoralis* (L.) shows a genetically determined polymorphism for shell colour (brown, pink or yellow) and banding pattern (up to five dark brown bands), which may serve a.o. as a protective colouration against visual predation (SHEPPARD, 1951 ; CAIN & SHEPPARD, 1954) and internal heating by solar radiation (GARCIA, 1977 ; HEATH, 1975 ; RICHARDSON, 1974 ; SEDLMAIR, 1956).

The aim of the present study was to ascertain the differential climatic selection by heat death on the populations of the Belgian coastal dune area. This was done by comparing the morph frequencies of intact dead shells with those of the live snails, on the assumption that the majority of the dead shells was the result of heat death (RICHARDSON, 1974, 1979).

2. MATERIALS AND METHODS

In September 1982, 22 colonies of *Cepaea nemoralis* were sampled throughout the Belgian coastal dune region. For a more detailed des-

Table 1

Collections of Cepaea nemoralis *from the Belgian coastal dune region : September 1982*

Locality	Live Dead	Yellow					Pink					Brown	Total	Habitat
		0	3	5	mv	EU	0	3	5	mv	EU	U		
De Panne	L	73	1	27	10	74	36	—	49	7	36	—	203	A + S
	D	13	1	12	4	15	6	—	16	4	6	—	56	A + S
Koksijde	L	64	6	19	4	72	5	1	6	—	6	1	106	S
	D	142	37	103	11	183	17	29	61	1	46	—	401	S
Oostduinkerke 1	L	53	1	52	5	54	5	1	31	2	6	—	150	A + S
	D	22	1	42	4	24	1	—	20	—	1	—	91	A + S
Oostduinkerke 2	L	70	—	10	7	70	4	—	—	—	4	—	91	H
	D	52	—	13	4	52	—	—	7	—	—	—	76	H
Oostduinkerke 3	L	18	48	42	6	66	6	23	11	2	29	34	190	S
	D	5	15	25	9	21	2	5	9	—	7	21	91	S
Oostduinkerke 4	L	13	35	19	3	48	—	7	1	—	7	18	96	A
	D	31	39	29	5	71	1	1	7	—	2	12	125	A
Oostduinkerke 5	L	—	6	16	7	8	—	21	64	9	23	—	123	A
	D	—	18	38	11	18	5	67	153	21	74	3	316	A
Oostduinkerke 6	L	—	6	29	3	6	—	9	55	1	9	—	103	A
	D	—	10	129	6	10	3	26	208	7	30	—	389	A
Nieuwpoort 1	L	4	49	28	4	56	4	76	37	7	81	6	215	H
	D	5	21	9	1	27	4	43	18	2	47	—	103	H
Nieuwpoort 2	L	—	10	17	3	10	—	19	47	2	19	—	98	H
	D	—	4	12	2	4	—	8	53	—	8	—	79	H
Nieuwpoort 3	L	—	1	16	4	4	—	8	31	3	9	—	63	R
	D	—	11	29	2	12	1	14	55	1	16	—	113	R

Westende	L	—	55	37	16	57	—	—	—	—	—	—	108	A
	D	2	29	25	3	31	—	—	—	—	—	—	59	A
Middelkerke	L	—	—	1	—	—	—	—	—	—	—	—	1	A
	D	—	—	2	2	—	4	—	—	—	—	—	4	A
Oostende	L	1	40	19	4	41	—	—	—	—	—	—	64	A
	D	—	4	—	—	4	—	—	—	—	—	—	4	A
Bredene 1	L	23	14	14	—	37	5	4	15	—	9	2	77	H
	D	—	8	5	—	8	3	3	8	1	6	—	28	H
Bredene 2	L	—	40	14	4	42	—	7	1	—	7	—	66	A
	D	—	13	4	—	13	—	—	—	—	—	—	17	A
De Haan 1	L	—	—	—	—	—	—	—	—	—	—	—	—	H
	D	—	5	22	—	5	—	1	2	—	1	—	30	H
De Haan 2	L	—	110	31	—	110	—	80	6	—	80	—	227	H
	D	2	45	18	2	47	1	60	12	—	61	—	140	H
Wenduine	L	4	118	28	—	122	—	15	4	—	15	—	169	A
	D	1	117	22	3	119	—	13	2	—	13	—	158	A
Blankenberge 1	L	1	79	10	1	80	—	21	5	—	21	—	117	A
	D	—	55	12	2	57	—	23	—	—	23	—	92	A
Blankenberge 2	L	38	18	10	—	56	1	—	1	—	1	—	68	A
	D	9	2	4	—	11	1	—	—	—	1	—	16	A
Zwin	L	4	71	9	1	75	18	2	2	—	20	—	107	A
	D	5	161	22	3	166	35	3	—	—	38	—	229	A

L : live snails ; D : dead-intact shells.

Banding morphs : 0 = 00000 ; 3 = 00300 ; 5 = 12345 ; mv : minor variations ; EU : effectively unbanded ; U : unbanded.

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

cription of the dune area and the geographical variation in polymorphism of *Cepaea* we refer to De Smet (1982). The samples were divided into four habitat categories :

A : mobile to semi-mobile dune mainly composed of *Ammophila arenaria* (L.) Link.

H : fixed dune characterized by an increased plant cover (a.o. *Ammophila arenaria* (L.) Link, *Phleum arenarium* L., *Festuca rubra* L.

S : scrub with *Hippophaë rhamnoides* L. and *Salix repens* L. being common.

R : areas with much *Rubus caesius* L. and *Rubus* spp. forming a closed habitat.

Shells of *C. nemoralis* were scored for shell colour, presence or absence of bands, number and position of bands and effectively unbandedness (Lamotte, 1951 ; Cain & Sheppard, 1954). Live snails were scored in the field and released ; dead-intact and predated shells were taken to the laboratory.

The significance of the differences in morph frequencies between the dead-intact shells and the live snails was tested by a RxC test of independence using the G-test (Sokal & Rohlf, 1973).

3. Results

Table 1 gives the morph frequencies, the number of live snails and dead-intact shells, and the habitat of each sample. Of the 22 samples, 20 could be tested by the G-statistic for significant differences in morph frequencies between dead-intact and live shells. The probability of independence for heat death was calculated for three morph classes : all morphs, colour and banding. The all morphs class contains, both for yellow (Y) and pink (P) coloured shells, unbanded (Y/P00000), mid-banded (Y/P00300), five-banded (Y/P12345), minor band variations (Y/Pmv) and effectively unbanded (Y/PEU) shells, and the brown unbanded morph (B00000). The colour class contains yellow, pink and brown shells irrespective of banding ; in the banding class the main banding morphs 00000, 00300, 12345, mv and EU are considered, irrespective of colour. The G-values, degrees of freedom and significance levels calculated for those three morph classes are shown in Table 2.

Only 4 (Oostduinkerke 6, Oostende, Blankenberge 2, Zwin) of the 20 samples showed no significant difference in morph frequency between dead-intact and live shells. The directions of the differences larger or equal to 5% found for the other samples are given in Table 3. It is clear that, although those directions are not always constant, some trends are apparent which we summarized in Table 4. The dark morphs, e.g. the pink colour class, the five-banded morph in general, and the pink and yellow five-banded shells are over-represented in dead-intact shells, whereas the lighter coloured morphs, e.g. the yellow-colour class, the unbanded, effectively unbanded shells and minor variants in general, and the yellow unbanded, minor variants, effectively unbanded and mid-banded shells are under-represented. An exception to these general trends are the brown unbanded shells which are under-represented in the dead shell samples.

Table 2

Results of G-test of independence on samples of live snails and dead-intact shells : G-value, degrees of freedom and significance

Locality	All morphs	Colour	Banding
De Panne	2.30, 6,n.s.	0.06, 1,n.s.	7.64, 3,*
Koksijde	34.20, 8,***	15.63, 2,***	26.20, 3,***
Oostduinkerke 1	10.62, 7,n.s.	2.15, 1,n.s.	6.64, 3,*
Oostduinkerke 2	17.74, 4,***	1.53, 1,n.s.	6.70, 2,*
Oostduinkerke 3	16.08, 8,*	1.46, 2,n.s.	8.46, 3,*
Oostduinkerke 4	19.26, 7,**	4.15, 2,n.s.	3.62, 3,n.s.
Oostduinkerke 5	7.48, 7,n.s.	2.21, 2,n.s.	7.10, 3,*
Oostduinkerke 6	5.94, 6,n.s.	0.02, 1,n.s.	3.78, 3,n.s.
Nieuwpoort 1	10.74, 8,n.s.	5.70, 2,*	1.90, 3,n.s.
Nieuwpoort 2	9.44, 5,*	1.36, 1,n.s.	6.56, 2,*
Nieuwpoort 3	10.76, 6,*	0.25, 1,n.s.	7.08, 3,*
Westende	8.46, 3,*	— —	8.46, 3,**
Oostende	3.64, 3,n.s.	— —	3.64, 3,n.s.
Bredene 1	67.32, 7,***	5.20, 2,*	11.26, 3,**
Bredene 2	17.14, 4,***	3.89, 1,*	1.90, 2,n.s.
De Haan 2	22.62, 6,***	7.14, 1,**	11.70, 3,**
Wenduine	7.28, 5,n.s.	0.27, 3,n.s.	6.90, 1,*
Blankenberge 1	10.30, 5,*	0.24, 1,n.s.	1.80, 3,n.s.
Blankenberge 2	3.40, 4,n.s.	0.36, 1,n.s.	1.86, 2,n.s.
Zwin	5.88, 6,n.s.	0.78, 1,n.s.	0.64, 3,n.s.

*** : $p < 0.005$; ** : $p = 0.025 - 0.005$; * : $p = 0.1 - 0.025$.

Table 5 shows the results of the G-test applied to the total collection of shells from the coastal dune area. From the summary of those data (Table 6) it follows that the general trends are similar as found earlier

Table 3

Differences ($\geqslant 5$ %) in morph frequency of dead-intact shells compared to live snails from the same locality

Locality	All morphs	Colour	Banding
De Panne	Y0^{o}, Y5^{+}, YEU^{o}, P0^{o}, P5^{+}, PEU^{o}		0^{o}, 5^{+}, mv^{+}, EU^{o}
Koksijde	Y0^{o}, Y5^{+}, YEU^{o}, P3^{+}, P5^{+}, PEU^{+}	Y^{o}, P^{+}	0^{o}, 3^{+}, 5^{+}, EU^{o}
Oostduinkerke 1	Y0^{o}, Y5^{+}, YEU^{o}		0^{o}, 5^{+}, EU^{o}
Oostduinkerke 2	Y0^{o}, Y5^{+}, YEU^{o}, P5^{+}	Y^{o}, P^{+}	0^{o}, 5^{+}, EU^{o}
Oostduinkerke 3	Y3^{o}, Y5^{+}, Ymv^{+}, YEU^{o}, P3^{o}, PEU^{o}, B0^{o}	B^{o}	3^{o}, 5^{+}, mv^{+}, EU^{o}
Oostduinkerke 4	Y0^{+}, Y3^{o}, YEU^{+}, P3^{o}, P5^{+}, PEU^{o}, B0^{o}	Y^{+}, B^{o}	3^{o}, 5^{+}, EU^{o}
Oostduinkerke 5			3^{+}, 5^{o}, EU^{+}
Oostduinkerke 6	Y5^{+}		3^{o}, 5^{+}, EU^{o}
Nieuwpoort 1	P3^{+}, PEU^{+}	Y^{o}, P^{+}	EU^{+}
Nieuwpoort 2	Y3^{o}, YEU^{o}, P3^{o}, P5^{+}, PEU^{o}	Y^{o}, P^{+}	3^{o}, 5^{+}, EU^{o}
Nieuwpoort 3	Y3^{+}, YEU^{o}		3^{+}, mv^{o}
Westende	Y5^{+}, Ymv^{o}		5^{+}, mv^{o}
Oostende	Y3^{+}, Y5^{o}, Ymv^{o}, YEU^{+}		3^{+}, 5^{o}, mv^{o}, EU^{+}
Bredene 1	Y0^{o}, Y3^{+}, YEU^{o}, P3^{+}, P5^{+}, PEU^{+}	Y^{o}, P^{+}	0^{o}, 3^{+}, 5^{+}, EU^{o}
Bredene 2	Y3^{+}, Ymv^{o}, YEU^{+}, P3^{o}, PEU^{o}	Y^{+}, P^{o}	3^{+}, mv^{o}
De Haan 2	Y3^{o}, YEU^{o}, P3^{+}, P5^{+}, PEU^{+}	Y^{o}, P^{+}	3^{o}, 5^{+}, EU^{o}
Blankenberge 1	Y3^{o}, YEU^{o}, PEU^{+}		
Blankenberge 2	Y3^{o}, YEU^{o}		0^{+}, 3^{o}, 5^{+}, EU^{o}
Zwin		P^{o}	

$^{+}$ = over-represented in dead shells ; ^{o} = under-represented in dead shells.
Y = yellow ; P = pink ; B = brown.
0 = 00000 ; 3 = 00300 ; 5 = 12345 ; mv = minor variations ; EU = effectively unbanded.

Table 4

Summary of differences ($\geqslant 5$ %) in morph frequency of dead-intact shells compared to live snails from the same locality

	Over-represented			Under-represented		
% Cases	All morphs	Colour	Banding	All morphs	Colour	Banding
100	P5			(P0) B0	Brown	
80 - 90	Y5		5	Y0		0
70 - 80		Pink		Ymv, YEU	Yellow	EU
60 - 70				Y3		mv
50			P3, PEU, 3			

Abbreviations as in Table 3. Difference occurring once is bracketed.

(Table 4) : especially higher numbers of dead-intact shells for the five-banded morphs, the pink and five-banded pink shells, and correspondingly lower numbers for the yellow morphs and the unbanded and midbanded shells in general.

Table 5

Differences in morph frequency for all live and all dead-intact shells : general survey

All morphs : $G = 106.84$; $df = 8$; $p < 0.005$

Morph	Live N	Live %	Dead-intact N	Dead-intact %	Total N	Total %
Y00000	366	15.0	289	11.0	655	12.9
Y00300	708	29.0	596	22.8	1304	25.8
Y12345	488	18.3	577	22.1	1025	20.3
Y min.var.	82	3.4	74	2.8	156	3.1
P00000	84	3.4	80	3.1	164	3.2
P00300	294	12.0	296	11.3	590	11.7
P12345	366	15.0	631	24.1	997	19.7
P min. var.	33	1.4	37	1.4	70	1.4
B00000	61	2.5	37	1.4	98	1.9
Total	2442	100.0	2617	100.0	5059	100.0

Colour : $G = 40.65$; $df = 2$; $p < 0.005$

Morph	Live N	Live %	Dead-intact N	Dead-intact %	Total N	Total %
Yellow	1604	65.7	1536	58.7	3140	62.1
Pink	777	31.8	1044	39.9	1821	36.0
Brown	61	2.5	37	1.4	98	1.9
Total	2442	100.0	2617	100.0	5059	100.0

Banding : $G = 89.72$; $df = 3$; $p < 0.005$

Morph	Live N	Live %	Dead-intact N	Dead-intact %	Total N	Total %
00000	511	20.9	406	15.5	917	18.1
00300	1002	41.0	892	34.1	1894	37.4
12345	814	33.3	1208	46.2	2022	40.0
min.var.	115	4.7	111	4.2	226	4.5
Total	2442	99.9	2617	100.0	5059	100.0

Live-dead shell comparisons of shells having five distinct bands with others showing band fusions, were performed on the accumulated data (Table 5). The ratio for shells without fusions to those with band fusions is $582/232 = 2.51$ for live snails ; for dead-intact shells this ratio is $722/486 = 1.49$. It follows that the over-representation of dead-intact five-bandeds in general, is largely due to the number of shells showing band-fusions ($G = 29.62$, $df = 1$, $p < 0.005$). The position of the fusions, e.g. at the lower or upper side of the shell, provokes an identical effect.

No simple relationship between the morph frequency of heat death snails and habitat could be demonstrated.

Table 6

Summary of differences in morph frequency of all dead-intact shells compared to all live snails

	Over-represented			Under-represented		
% Difference	All morphs	Colour	Banding	All morphs	Colour	Banding
> 10	—	—	5	—	—	—
5 - 10	P5	Pink	—	—	Yellow	0.3
1 - 5	Y5	—	—	Y0, Y3, B0	Brown	—
< 1	—	—	—	Ymv, P0, P3, Pmv	—	mv

Abbreviations as in Table 3.

4. Discussion

As *Cepaea nemoralis* is a poikilothermic animal, its body heat is primarily derived from the external environmental energy, principally solar radiation. The pigmentation of the shell plays an important role in the absorption of the heat radiation. Laboratory experiments have demonstrated that differences among the shell morphs may lead to an increased ability of the dark coloured and banded snails to use solar radiation for raising body temperature. In his study on the albedo of empty shells, Richardson (1974) showed that yellow unbanded shells reached a temperature of 1 to 2°C lower than that attained by pink banded shells. Heath (1975) measured temperature differences of about 1°C between light and dark coloured, and banded and unbanded mercury filled shells or live snails, the equilibrium temperature of the darkerpigmented shells being almost always higher than the lighter ones. By exposing live snails and agar-filled shells to natural and artificial sunlight, GARCIA (1977) reached similar conclusions and found temperature variations of about 1-2.5°C with phenotype.

The upper lethal temperature for short periods of exposure (0.5 h) is about 43°C (RICHARDSON, 1974); GARCIA (1977) reports an important mortality after artificial heating by illumination for 5 hours at 40-41.5°C. Temperatures near the upper lethal limit are regularly measured at the surface of the sand dunes and between the vegetation near the ground (ANTEUNIS, 1956).

The different body temperatures that can be attained by the light and dark coloured snails, may produce differences in metabolism, growth, reproduction and mortality, likewise in activity and behaviour. Although there exist genetically determined population differences in the physiology of *C. nemoralis*, WOLDA (1967) found that in experimental populations oviposition frequency was higher for yellow snails than for pink snails when raised at 20°C but not at 12°C. The mortality of the yellow unbanded snails was lower than for the other morphs at 20°C. The experimental results of BOETTGER (1954), SEDLMAIR (1956) and LAMOTTE (1966) are similar and indicate that yellow *Cepaea* have a higher temperature tolerance than pink individuals, and that unbanded snails are more resistant than banded ones.

RICHARDSON (1979), studying the morph frequencies of empty intact shells on sand dunes in south-west England, found that yellow and unbanded shells tended to be under-represented in dead shell collections, while pink and mid-bandeds were over-represented. He also noted an under-representation of five-banded shells in general, and suggested that the extreme dry and warm summer of 1976 may have caused a heavier, less-selective mortality than a normal year.

Our findings on heat death for natural populations of *C. nemoralis* from the Belgian coastal dune area, e.g. over-representation of dead five-banded and pink shells, and under-representation of dead yellow unbanded, midbanded and effectively unbanded shells, are in good agreement with the results obtained under laboratory conditions. The hypothesis of a greater susceptibility for heat death by the darker morphs, is also confirmed by the high mortality for shells with band-fusions among the five-bandeds. The figures for the brown snails are unexpected since they show a tendency to be under-represented in dead shell collections. We have some indications that this phenomenon could be explained by differences in daily activity. Sampling the colonies Oostduinkerke 3 and 4, in the early morning, it was noted that most of the brown snails were already inactive and sheltered in the vegetation when the other morphs were still crawling around. Brown shells probably not only have an earlier onset of early morning activity due to their faster heating up by the absorption of solar radiation, as demonstrated for *Cepaea vindobonensis* (Jones, 1973), but may likewise show a stronger reduction of daytime activity in the higher temperature ranges (Cameron, 1970b), compared to the other morphs, thereby reducing the risk of heavy waterloss on dry and sunny days.

The simultaneous action of temperature and relative humidity largely determines the survival, activity and distribution of helicid snail in various ways (Cameron, 1970a, b). Other climatic factors significant to the organisms are radiation, wind and vapour pressure. Climate has been suggested as the main causal factor for the overall distribution of the shell and banding polymorphism of the Belgian sand-dune populations of *C. nemoralis* (De Smet, 1982). The present contribution shows that selective pressure by radiation may play an important part in determining the high proportions of the unbanded morph in general and the yellow unbanded in particular, in the most arid stretch of the southern dune region. Likewise could the thermal advantage enjoyed by the morphs with band-fusions explain their higher frequency in the northern half of the dune area with highest mean annual precipitation. The concentration of the brown-shelled individuals in the complex dunes, known to accumulate cold air during the night, probably also results from a selective advantage associated with solar radiation.

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