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POPULATIONS OF *CEPAEA HORTENSIS* (O. F. MÜLLER, 1774) POLYMORPHIC FOR THE COLOUR OF SHELL LIP IN NORTH-WESTERN POLAND AND NORTH-CENTRAL GERMANY

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ABSTRACT: In *Cepaea hortensis* (O. F. Müller), the shell lip (peristome) is usually white. In most areas the lip colour allows us to reliably distinguish this species from *C. nemoralis* (Linnaeus) in which the lip is usually dark brown. Populations polymorphic for lip colour are rare and occur only locally. Here I report on populations of *C. hortensis* containing dark-lipped individuals in north-western Poland and in north-central Germany. The frequency of dark-lipped individuals ranged from 3% to 31%. It was common in brown and pink shells, but occurred only sporadically in yellow shells. No selective factors promoting dark-lipped *C. hortensis* are evident. The occurrence of this phenotype is likely to reflect random events.

KEY WORDS: colour polymorphism, land snails, population genetics, random events

INTRODUCTION

Land snail species in the genus *Cepaea* are readily recognised by the colour of shell lip (peristome). In *C. nemoralis* (Linnaeus, 1758) the lip is dark brown, in *C. hortensis* (O. F. Müller, 1774) it is white, and in *C. vindobonensis* (Férussac, 1821) it is pinkish-brown. *C. silvatica* (Draparnaud, 1801) is similar to *C. vindobonenesis*, but is restricted in its distribution to the Western Alpine/Jura region. The diagnostic value of lip colour is especially useful in distinguishing between *C. nemoralis* and *C. hortensis* which share a very similar shell polymorphism. In fact, in places where they co-occur, only mature individuals with developed lips can be assigned to either species.

Although very useful in most areas, the colour of the lip is not entirely reliable as diagnostic tool. In some areas populations of *C. nemoralis* contain white-lipped individuals, and populations of *C. hortensis* contain dark-lipped ones (no data exist for *C. vindobonensis* and *C. silvatica*). Populations of *C. nemoralis* polymorphic for lip colour occur locally in England (ARNOLD 1968, COOK 2003), Ireland (COOK & PEAKE 1960, 1962), and the Pyrenees (ARNOLD 1968). In *C. hortensis*, high frequencies of dark-lipped individuals occur in central France (GUERRUCCI 1973a), and locally in England (R. A. D. CAMERON, personal communication). This phenotype has not been recorded from other parts of the species distribution and is apparently rare.

The mode of inheritance of various shell characteristics in *C. nemoralis* and *C. hortensis* is largely known and is parallel in both species (MURRAY 1975). The loci for shell colour, presence or absence of bands, and band and lip colour are tightly linked; linkage disequilibria are common in many populations (JONES et al. 1977). Dark lip colour is dominant over white lip colour, in both *C. nemoralis* (MURRAY 1975) and *C. hortensis* (GUERRUCCI 1973b).

In this paper I report on localised populations of *C. hortensis* containing dark-lipped individuals in north-western Poland and in north-central Germany.

MATERIAL AND METHODS

STUDY AREA AND HABITAT TYPES

I found populations of *C. hortensis* containing dark-lipped individuals in two areas studied as parts of larger surveys. Area 1 lies in north-western Poland, where an extensive study of *C. nemoralis* and *C. hortensis* polymorphism has been conducted since 2002. In this area, *C. hortensis* is locally common. I found populations of this species in the vicinity of Darłowo, Gdynia, Jasień, Lębork, Miastko, Piła, Puck, Tuchola and Ustka. Populations in the village Kawcze (centered on 54°04'06"N, 16°53'12"E) near Miastko were the only ones where dark-lipped *C. hortensis* occurred. Area 2 lies within a study area extending along 52°N parallel from Biała Podlaska in Poland to Rotterdam in the Netherlands. Samples were taken at the crossing of the 52°N parallel with consecutive meridians. The area between Midlich (centered on

Table 1. Frequencies of shell and lip colour in *Cepaea hortensis* and geographic coordinates of sampling sites in Area 1. Habitat type: O – open, SO – semiopen

Site No	Habitat type	Sample size	Frequency (%) of shell colour			Frequency (%) of shells with dark lip				Latitude N	Longitude E
			Brown	Pink	Yellow	All	Brown	Pink	Yellow		
1	SO	36	14	0	86	11	80	–	0	54.0781	16.8881
2	SO	62	10	0	90	10	100	–	0	54.0747	16.8664
3	SO	43	9	0	91	9	75	–	0	54.0781	16.8875
4	SO	54	13	0	87	7	57	–	0	54.0761	16.8764
5	O	111	10	0	90	7	73	–	0	54.0761	16.8767
6	O	54	11	0	89	6	50	–	0	54.0758	16.8764
7	SO	38	2.5	2.5	95	5	100	100	0	54.0750	16.8756
8	SO	79	4	0	96	4	100	–	0	54.0744	16.8753

Table 2. Frequencies of shell and lip colour in *Cepaea hortensis* and geographic coordinates of sampling sites in Area 2. Habitat type: O – open, SO – semiopen, S – shaded

Site No	Habitat type	Sample size	Frequency (%) of shell colour			Frequency (%) of shells with dark lip				Latitude N	Longitude E
			Brown	Pink	Yellow	All	Brown	Pink	Yellow		
1	SO	124	26	6	68	31	100	88	0	52.0522	9.1006
2	SO	26	12	8	80	19	100	100	0	51.9997	7.1969
3	O	85	1	2	97	15	100	100	12	51.9628	9.9744
4	O	56	2	7	91	11	100	50	6	51.9633	9.9739
5	O	124	6	6	88	10	63	100	1	51.9456	11.0308
6	O	180	0	1	99	8	–	100	7	51.9956	9.9514
7	O	45	2	9	89	4	100	25	0	51.9997	7.1967
8	O	33	0	3	97	3	–	100	0	51.9800	10.9881
9	O	11	0	0	100	0	–	–	–	52.0717	7.1453
10	O	22	0	4	96	0	–	–	–	52.0347	7.1422
11	S	35	0	0	100	0	–	–	–	52.0408	9.9344
12	O	40	0	0	100	0	–	–	–	52.0922	10.0500
13	O	45	0	0	100	0	–	–	–	52.0178	10.0061
14	O	20	0	0	100	0	–	–	–	51.9861	10.0228
15	SO	32	0	3	97	0	–	–	–	52.0683	11.0994
16	SO	17	0	0	100	0	–	–	–	52.1092	11.0572
17	O	100	0	0	100	0	–	–	–	52.1094	11.0572
18	O	85	0	0	100	0	–	–	–	51.9536	11.1639
19	O	131	0	7	93	0	–	–	–	51.9081	11.0408
20	O	74	0	0	100	0	–	–	–	51.9522	11.1611

Fig. 1. *Cepaea hortensis* with dark lip (photo M. OŻGO)

52°00'32"N, 07°11'29"E) and Halberstadt (centered on 51°53'28"N, 11°03'30"E) was the only one along this transect where I found dark-lipped *C. hortensis*. Geographic coordinates of sampling sites in Area 1 and 2 are given in Tables 1 and 2.

Habitats were divided into three categories: open, semi-open, and shaded. In shaded habitats, trees or shrubs were dense enough to give shade throughout the day; in open habitats vegetation consisted of grasses and herbs; semi-open habitats were intermediate in character, with scattered shrubs or trees.

SAMPLE COLLECTION AND SCORING

Collections in Area 1 were carried out in 2008–2009, in Area 2 in 2008. The snails were collected from areas of approximately 100–1000 m^2 covered with relatively uniform vegetation. Only live mature individuals were included. Many populations were small and samples were difficult to obtain; populations in which less than 10 mature individuals could be found were omitted. I scored the ground colour of the shells as yellow, pink or brown, and the lip as white or dark. The colour of the lip in dark-lipped snails was light brown or pink, and was never as dark as it usually is in *C. nemoralis* (Fig. 1). In some areas it is quite common for brown unbanded shells to leak a little pigment into the lip, giving it a slightly purplish-brown appearance, which is not evenly distributed all over the lip, whereas in pink and yellow shells with dark lips, the colour is more or less evenly distributed. This might mean that not all brown shells recorded with dark lips show the same allele that is present in pink and yellow shells (R. A. D. CAMERON, personal communication). In the samples analysed here, in most brown shells the pigment was evenly distrib-

uted over the lip, but I scored as dark-lipped all shells in which the colour in the lip appeared, as opposed to clearly white-lipped shells. After scoring the snails were returned to the site.

RESULTS

Area 1. Dark-lipped *C. hortensis* were present in all 8 populations and constituted 4% to 11% of the snails (Table 1). The dark lip phenotype was present in 75% of brown shells (data combined for all populations), and did not occur in yellow shells. There was just one pink-shelled snail, and it had a dark lip. No association of shell or lip colour with habitat type is apparent.

Area 2. Dark-lipped *C. hortensis* were present in 8 out of 20 populations and constituted 3% to 31% of the snails (Table 1). The dark lip phenotype was common in brown and pink shells but occurred only sporadically in yellow shells (present in 93% of brown, 79% of pink, and 4% of yellow shells, data combined for all populations in which dark lip occurred). Dark lip in yellow shells occurred only in those populations in which pink and/or brown snails with dark lip were also present. In 12 populations there were no dark-lipped snails. In nine of them, all shells were yellow. In the remaining three, there were no brown shells, and pink ones were uncommon (in samples 4 and 13 they were represented by just one shell). No association of shell or lip colour with habitat type is apparent.

DISCUSSION

In this study I report on the occurrence of the dark lip phenotype in populations of *C. hortensis* inhabiting two relatively small areas. Both lie within much larger areas in which survey studies were conducted, and in which no other dark-lipped *C. hortensis* were found. This indicates that the phenotype dark lip is uncommon and occurs only locally.

Dark lip was common in brown and to a lesser extend in pink shells. In yellow shells it occurred sporadically, and only in those populations in which dark-lipped brown or pink shells were also present. This suggests that the allele for dark lip was linked in most cases with the allele for brown and for pink ground colour of the shell. In yellow-shelled snails dark lip was probably present as a result of recombination between closely linked genes. This conclusion is supported by data from Wiltshire, GB, where a strong linkage of dark lip with pink shells, frequently with 100% segregation, was also found. Out of 138 samples, 125 contained dark lip in pink and in most all the pinks were dark lipped. Only one sample had an excess of dark lip in yellow (R. A. D. CAMERON, personal communication).

A variety of evolutionary forces have been proposed to affect shell polymorphism in *Cepaea* snails (for reviews see e.g. JONES et al. 1977, COOK 1998, OŻGO 2008). Lip colour polymorphism is possibly the most enigmatic. A possible explanation is climatic selection. In *C. nemoralis,* an association of high frequencies of white-lipped snails with wet areas and dark-lipped ones with dry areas was observed in the Pyrenees (ARNOLD 1968). Association of white lip phenotype with wet climate in *C. nemoralis* and dark lip with dry climate in *C. hortensis* was suggested by JONES et al. (1977), but with no concrete data. Also, no mechanism of selection was indicated (JONES et al. 1977). Climatic selection has been shown to affect frequencies of colour and banding morphs in *Cepaea* snails (e.g. ARNOLD 1968, JONES 1973, JONES et al. 1977, OŻGO 2005, OŻGO & KINNISON 2008, CAMERON & POKRYSZKO 2008, OŻGO & KOMOROWSKA 2009). Dark shelled snails heat up faster and reach higher internal temperatures than light shelled ones. When the incoming radiation is sparse, this has beneficial effect on activity, growth and fecundity, and puts dark snails at selective advantage. However, under severe heat load they can be at greater risk of overheating and dessication (HEATH 1975, CHANG 1991). Although climatic selection might provide an explanation for the shell lip polymorphism, I do not think it is very likely, especially not in *C. hortensis*. In this species, the shells scored as dark-lipped often have only a flush of dark colour on the inner part of the lip. This part is not exposed to solar radiation in live animals, and thus cannot affect their thermal properties and respond to climatic selection.

In this study the occurrence of dark lip phenotype was very localised, with no conceivable effect of large-scale climatic factors. Also, there was no association with habitat type. In France, where this phenotype is common over wide areas, the same frequencies occur in very different climatic zones, which also renders climatic explanation not very likely (GUERRUCCI 1973a). These findings strongly suggest the effect of random events: local mutation or immigration, and subsequent spreading of the rare allele to nearby populations. Curiously, it can persist over long periods of time. In a modern, living sample of *Cepaea*

hortensis in Wroxeter (Shropshire) dark lip is present. It is also present in subfossil snails from an abandoned Roman city being dug up in the same field. The phenotype seems to have persisted locally for at least 1,700 years (R. A. D. CAMERON, personnal communication).

When colour is under genetic control, phenotype can serve as a marker for genotype. In the case of *C. hortensis*, the lip colour might serve as a readily scorable neutral genetic marker. Its spatial distribution provides an opportunity to study the effects of chance events on genetic composition of populations.

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