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POLYMORPHISM OF THE INTRODUCED SNAIL *CEPAEA NEMORALIS* (GASTROPODA, HELICIDAE) FROM TWO DISTANT PARTS OF EASTERN EUROPE: ACCIDENTAL SIMILARITY OR REGULARITY?

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Polymorphism of the Introduced Snail *Cepaea nemoralis* (Gastropoda, Helicidae) from two Distant Parts of Eastern Europe: Accidental Similarity or Regularity? Gural-Sverlova, N. V., Gural, R. I. — The shell coloration of *Cepaea nemoralis* (Linnaeus, 1758) from Western Ukraine (Ivano-Frankivsk, Lviv, and Ternopil Regions) and from the Moscow Region of Russia was analyzed, in total, almost 6 thousand specimens from 32 sites. In the samples from the Moscow Region, on average, there were half as many yellow shells and four times as many pink mid-banded shells. There were no other statistically significant differences. As in other areas of Eastern Europe, yellow unbanded and brown shells were often absent or represented by few individuals in both compared areas, and brown banded shells were completely (Western Ukraine) or almost completely (Moscow Region) absent, which may be related to the founder effect. Analysis of the literature data showed that in the introduced populations of *C. nemoralis* from Europe and USA, a distinct predominance of one or two of the 4 light phenotypes (yellow unbanded, yellow mid-banded, pink unbanded, and pink mid-banded) is often observed. The total frequency of these phenotypes in introduced populations is often higher than its average values calculated for different parts of the natural range. A possible relationship between the observed pattern and climatic selection is discussed.
Key words: land mollusks, grove snail, phenotypic composition, climatic selection, Western Ukraine, Moscow Region, European Russia.

Introduction

Cepaea nemoralis (Linnaeus, 1758) is one of the best-known species of European land mollusks; many publications are devoted to the color and banding polymorphism of its shells. Long-term studies in England, France, Germany and other European countries already in the second half of the 20th century proved that the phenotypic composition of populations of this species is the result of a complex interaction of selective and non-selective (stochastic) factors (Jones et al., 1977). The influence of both mentioned groups of factors can theoretically be enhanced in the introduced populations of *C. nemoralis* (Sverlova, 2007) and related species *Cepaea hortensis* (O. F. Müller, 1774) (Gural-Sverlova & Gural, 2018) that live at a considerable distance from the main part of their present ranges. On one hand, the initial restriction of genetic and phenotypic diversity, caused by a limited number of founding individuals and the possibility of accidental disappearance of some traits in the initial stages of introduction, cannot be compensated for by immigration, but only by repeated introduction of the snails by people from the main part of the range or from other introduced populations.

On the other hand, introduced populations are often forced to adapt to climatic conditions not typical for the species, which may enhance the influence of climate selection on their peculiar phenotypic structure, initially determined by the founder effect. Therefore, the phenotypic composition of each introduced population *C. nemoralis* can be considered a result of a microevolutionary experiment, beginning with the intentional introduction (Egorov, 2018; Howe, 1898) or unintentional transfer of snails, for example, with ornamental plants (Alexander, 1952; Bąkowski, 1880).

Recently, more and more reports have appeared not only about the finds of *C. nemoralis*, but also about the shell color and banding polymorphism of this species in Ukraine (Gural-Sverlova et al., 2020), Belarus (Kolesnik & Kruglova, 2016; Ostrovsky & Prokofieva, 2017) and in the European part of Russia (Gural-Sverlova & Egorov, 2021; Mukhanov & Lisitsyn, 2018; Sverlova, 2007). A lot of data regarding this issue has been accumulated in the laboratory of malacology of the State Museum of Natural History of the National Academy of Sciences of Ukraine in Lviv (hereinafter referred as SMNH NANU). This allows a preliminary comparison of quantitative data from different parts of Eastern Europe both with each other and with similar data for other parts of the present range of *C. nemoralis*, significantly expanded due to anthropochory, which became the main purpose of this publication.

Material and methods

The article uses data on shell coloration in almost 6 thousand individuals of *C. nemoralis* collected in Moscow Region of Russia (from 2006 to 2020) and in three administrative regions in Weastern Ukraine (2019–2020). All samples from Moscow Region and part of materials from Western Ukraine are stored in the malacological collection of SMNH NANU. The collecting sites are described below, and they are arranged in alphabetical and numerical sequence of their codes.

IF-1: Ukraine, Ivano-Frankivsk Region, Ivano-Frankivsk City, Halytska street, 48°56´49.6″ N 24°41´48.2″ E, 2019.

IF-2: Ivano-Frankivsk Region, Tysmenytsia District, Uhryniv village, Pol´ova street, between 48°57´25.3″ N 24°41´26.1″ E and 48°57´28.3″ N 24°41´25.4″ E, 2019.

IF-3: Ivano-Frankivsk Region, Bohorodchany District, Bohorodchany urban-type settlement, Shevchenko street, between 48°48´39.6″ N 24°32´29.1″ E and 48°48´46.3″ N 24°32´35.2″ E, 2019.

IF-4: ibidem, opposite side of Shevchenko street, 48°48´46.9″N 24°32´34.3″E, 2019.

L-1: Ukraine, Lviv Region, Lviv City, Horodotska street near the exit to the ring road, between 49°49´14.7″ N 23°54´56.6″ E and 49°49´17.0″ N 23°55´09.6″ E, 2020.

L-2: ibidem, Liubinska street, near the old airport terminal, 49°48´59.5″ N 23°57´19.6″ E, 2020.

L-3: ibidem, Liubinska street, on the former territory of a military unit, 49°49´08.5″ N 23°57´36.0″ E, 2020.

L-4: ibidem, Syhnivka street, 49°49´ 31.4″ N 23°57´27.9″ E, 2020.

L-5: ibidem, Liutneva street, 49°49´33.0″ N 23°57´43.1″ E, 2020.

L-6: ibidem, near the intersection of Horodotska street with Bahrianyi street and Rivna street, between 49°49´48.4″ N 23°58´35.2″ E and 49°49´54.9″ N 23°58´33.8″ E, 2020.

L-7: ibidem, near the intersection of General Chuprynka street with Makovei street and Tsehelskyi street, between 49°49´21.5″ N 24°00´00.1″ E and 49°49´18.5″ N 24°00´02.8″ E, 2020.

L-8: ibidem, Chervona street, between 49°49´25.3″ N 24°00´24.6″ E and 49°49´30.9″ N 24°00´25.0″ E, 2020.

L-9: ibidem, Vitovskyi street, between 49°49´47.1″ N 24°01´35.8″ E and 49°49´48.8″ N 24°01´32.5″ E, 2020.

L-10: ibidem, Kalicha Hora street, between 49°50´05.4″ N 24°01´37.6″ E and 49°50´07.7″ N 24°01´33.6″ E, 2019–2020.

L-11: ibidem, Hnatiuk street, 49°50´29.8″ N 24°01´21.0″ E, 2020.

L-12: ibidem, between Zelena street and Krymska street, between 49°49´28.6″ N 24°02´41.0″ E and 49°49´27.8″ N 24°02´56.9″ E, 2019–2020.

L-13: ibidem, Chmola street, near the former garden center, between 49°48´52.1″ N 24°01´30.2″ E and 49°48´52.6″ N 24°01´12.6″ E, 2019–2020.

L-14: ibidem, Khutorivka street, wasteland next to the garden center, between 49°47´58.8″ N 24°02´07.4″ E and 49°47´58.9″ N 24°02´02.6″ E, 2020.

L-15: Lviv Region, Pustomyty District, Zubra village, wasteland between 49°46´42.7″ N 24°03´08.4″ E and 49°46´43.4″ N 24°03´01.4″ E, 2019–2020.

M-1: Russia, Moscow Region, Moscow City, Severnyi administrative District, Lianozovski forest-park, coordinates of the main sampling place 55°54´06.0″ N 37°34´22.2″ E, 2015–2018.

M-2: ibidem, Yugo-Zapadnyi administrative District, Kotlovka municipal District, 55°39´57.6″ N 37°35´48.6″ E and between 55°40´03.0″ N 37°35´58.2″ E and 55°40´05.4″ N 37°36´03.0″ E, 2016.

M-3: Moscow Region, Dmitrov District, Dmitrov town, Pochtovaya street (56°20´26.4″ N 37°30´58.2″ E) and Professional´naya street (56°20´49.8″ N 37°31´05.4″ E), 2014-2017.

M-4: Moscow Region, Dolgoprudnyi town, near the garden center “Medra”, 55°56´30.6″ N 37°32´06.6″ E, 2017.

M-5: ibidem, Sheremetievski microdistrict, corner of Pervomaiskaya street and Komarova street, 55°59´33.6″ N 37°29´35.4″ E, 2017 and 2019.

M-6: Moscow Region, near the town of Lobnya, a sawmill in the forest, 55°59´37.8″ N 37°25´50.4″ E, 2018–2020;

M-7: Moscow Region, Lyubertsy District, Malakhovka urban-type settlement, Kirov street (55°38´33.6″ N 37°59´52.8″ E) and Fevral´skaya street (55°38´34.2″ N 37°59´39.6″ E), 2015–2017.

M-8: Moscow Region, Mytishchi District, Mytishchi town, Zapadnaya street, between 55°53´37.2″ N 37°42´12.6″ E and 55°53´38.4″ N 37°42´18.0″ E, 2017–2018.

M-9: Moscow Region, Krasnogorsk District, Nakhabino urban-type settlement, Panfilov street, 5 sites between 55°50´16.2″ N 37°10´46.2″ E, 55°50´10.2″ N 37°10´53.4″ E, 55°50´05.4″ N 37°10´40.8″ E and 55°50.22´ N, 37°10.57´ E designated as Nos. 1–4 and 7 in a previous publication (Gural-Sverlova & Egorov, 2021: fig. 2), 2006, 2017–2018.

M-10: ibidem, opposite side of Panfilov street, 2 sites between 55°50´13.2″ N 37°10´34.2″ E and 55°50´13.2″ N 37°10´34.2″ E designated as Nos. 5 and 6 in a previous publication (Gural-Sverlova & Egorov, 2021: fig. 2), 2017.

M-11: Moscow Region, Pushchino town, Park Pobedy (Victory Park), 54°50´16.2″ N 37°36´49.8″ E, 2016.

M-12: Moscow Region, Schelkovo District, Zagoryanski urban-type settlement, Zelenaya street (55°55´28.2″ N 37°55´14.4″ E), Kooperativnaya street (55°55´32.4″ N 37°55´00.0″ E) and Lenin street (55°55´28.8″ N 37°54´56.4″ E), 2016, 2018.

T-1: Ukraine, Ternopil Region, Chortkiv District, Chortkiv town, Zaliznychna street, 49°01´32.1″ N 25°47´34.9″ E, 2020.

More detailed descriptions and images of some of the above-mentioned sites were given in previous publications (Egorov, 2018; Gural-Sverlova & Egorov, 2021; Gural-Sverlova et al., 2020). Most of the samples from Western Ukraine were collected personally by the authors of the article. Other collectors are listed in Acknowledgments.

In Lviv and Ivano-Frankivsk Regions, where *C. nemoralis* usually lives together with another introduced species of the same genus, *C. hortensis*, only live adult snails were counted, less often their empty shells with well-preserved coloration. In other cases, to obtain more representative samples, immature individuals with a shell diameter of at least 1 cm were also collected.

For each shell, the ground color designated as “Y”(yellow, relatively few white shells were also included in this group), “P” (pink) or “B” (brown) as well as the banding type were determined:

1) unbanded shells — completely without bands, occasionally with 1–2 indistinct bands (modifications);

2) mid-banded — similarly for shells with one central band;

3) three-banded — the phenotypes with three lower bands, occasionally with traces of one or both upper bands;

4) five-banded — a group of phenotypes with 5 discrete or fused bands, occasionally with the absence of one band.

For samples containing at least 40 specimens, the frequencies of the following inherited traits (Murray, 1975) were calculated:

1) different ground color of the shell (yellow, pink or brown);

2) complete absence of bands on the shell;

3) absence of all bands, except for the central one, on banded shells;

4) absence of two upper bands on multi-banded shells.

We also calculated the frequencies of phenotype groups distinguished by the combination of the shell ground color and the banding type.

Results

The polymorphism in the shell banding type was registered at all studied sites, and such in the shell ground color at almost all sites, except for M-5 (table 1). However, brown shells were more often absent, and in other cases they were almost exclusively unbanded. Among the main types of shell banding (unbanded, mid-banded, three-banded, and five-banded), the samples most often lacked shells with three lower bands: at 42 % of studied sites in the Moscow Region and at 45 % of sites in Western Ukraine.

At almost all sites, all banded shells had dark, evenly pigmented bands. In Lviv, single individuals with depigmented (hyalozonate) or light colored bands were found. Adult snails of this coloration also had light edges of the aperture, not typical for *C. nemoralis* — from pinkish to white. The most original in this respect was the only sample from the Ternopil Region, in which about 26 % of the banded shells had unevenly pigmented bands, with alternating lighter and darker fragments, which in some cases gave the impression of spotty bands. Among the yellow banded shells, there were even more such specimens, about 41 %.

Table 1. The phenotypic composition of the studied samples

Site codes	Localities	Phenotype groups									Total
		Y-0	Y-1	Y-3	Y-5	P-0	P-1	P-3	P-5	B-0	
Western Ukraine, Ivano-Frankivsk Region											
IF-1	Ivano-Frankivsk	–	+	–	–	**9**	3	–	–	–	12
IF-2	Uhryniv	–	–	1	1	2	+	–	**3**	–	7
IF-3	Bohorodchany	–	–	–	29	**66**	–	–	–	–	95
IF-4	Ibidem	–	3	–	58	97	5	–	**196**	–	359
Total for this region		–	3	1	88	174	8	–	199	–	473
Western Ukraine, Lviv Region											
L-1	Lviv	4	282	66	–	**590**	186	39	–	–	1167
L-2	Ibidem	–	4	–	19	**294**	19	–	52	–	388
L-3	Ibidem	1	28	–	17	**37**	5	–	7	–	95
L-4	Ibidem	–	+	–	**4**	–	1	1	1	–	7
L-5	Ibidem	–	**9**	–	1	–	**9**	–	1	–	20
L-6	Ibidem	–	**48**	–	28	–	8	–	6	–	90
L-7	Ibidem	**17**	–	10	12	1	–	3	7	–	50
L-8	Ibidem	–	1	7	12	**19**	1	4	7	–	51
L-9	Ibidem	12	4	1	13	2	1	1	–	**17**	51
L-10	Ibidem	–	4	13	24	**33**	5	7	14	3	103
L-11	Ibidem	–	–	–	10	**48**	–	–	7	–	65
L-12	Ibidem	**13**	7	4	6	6	9	7	8	–	60
L-13	Ibidem	5	120	23	**291**	73	66	27	127	–	732
L-14	Ibidem	–	**63**	5	–	–	18	8	–	13	107
L-15	Zubra	**23**	9	–	18	1	–	–	2	–	53
Total for this region		75	579	129	455	1104	328	97	239	33	3039
Western Ukraine, Ternopil Region											
T-1	Chortkiv	3	6	34	28	2	5	**77**	69	–	224
Total for Western Ukraine		78	588	164	571	1280	341	174	507	33	3736
Russia, Moscow Region											
M-1	Moscow	1	94	–	96	66	87	1	**102**	–	447
M-2	Ibidem	11	1	–	1	**14**	1	–	10	13	51
M-3	Dmitrov	–	3	–	–	26	**114**	–	17	–	160
M-4	Dolgoprudnyi	3	10	6	**100**	21	16	18	72	–	246
M-5	Ibidem	–	–	–	–	–	**31**	9	4	–	44
M-6	Lobnya	1	1	9	1	**15**	1	–	–	–	28
M-7	Malakhovka	–	2	–	3	–	14	–	**25**	22	66
M-8	Mytishchi	–	37	8	39	**94**	21	2	26	1	228
M-9	Nakhabino	–	7	99	144	**318**	–	–	–	–	568
M-10	Ibidem	–	8	2	18	28	4	9	9	**34**	112
M-11	Pushchino	–	**3**	–	2	1	2	–	2	–	10
M-12	Zagoryanski	1	1	–	1	3	22	–	35	**88**	152*
Total for this region		17	167	124	405	586	313	39	302	158	2112*
Grand total		95	755	288	976	1866	654	213	809	191	5848*

Note. B-0 — brown unbanded; P-0 — pink unbanded; P-1 — pink mid-banded; P-3 — pink three-banded; P-5 — pink five-banded; Y-0, Y-1, Y-3 and Y-5 — the same for yellow shells; *taking into account one brown mid-banded shell from Zagoryanski; + recorded only in juveniles. The most common coloration variant in each sample is shown in bold.

A shell with similar "punctate" bands is shown in Richards et al. (2013).

In Moscow Region, the higher mean frequencies in the samples (table 2) had, in descending order, pink mid-banded, pink unbanded, pink five-banded, brown unbanded, and yellow five-banded shells (table 2). In Western Ukraine, this order was slightly different (pink unbanded, yellow five-banded, yellow mid-banded, pink five-banded), mainly due to the greater number of yellow and fewer pink mid-banded shells (see below).

In both compared parts of Eastern Europe, the frequencies of phenotype groups and separately considered phenotypic traits (table 2) vary greatly between sites. Statistically significant differences between Western Ukraine and Moscow Region were found only for the mean frequencies of yellow as well as pink mid-banded shells. In the samples of *C. nemora-*

Table 2. Frequencies of inherited coloration traits and phenotype groups in the compared areas

Traits / Phenotype groups	Western Ukraine		Moscow Region, Russia		Differences (Mann-Whitney test)
	min–max	mean	min–max	mean	
Phenotype groups distinguished by the combination of shell grund color and banding*					
Y-0	0–43.4	7.9	0–21.6	2.4	58
Y-1	0–58.9	14.3	0–21.0	5.7	96.5
Y-3	0–20.0	5.2	0–17.4	2.5	57
Y-5	0–39.8	19.3	0–40.7	12.8	56
P-0	0–75.8	27.1	0–56.0	19.1	90
P-1	0–16.8	5.5	0–71.3	21.8	45****
P-3	0–34.4	5.2	0–20.5	3.7	67.5
P-5	0–54.6	12.5	0–37.9	17.2	59.5
Inherited traits (shell grund color)					
Yellow	5.9–94.5	46.7	0–48.4	23.4	37****
Pink	5.7–94.1	50.3	39.5–100	61.8	68
Brown	0–33.3	3.0	0–58.6	14.8	73
Inherited traits (absence of all or part of the bands)					
Unbanded	0–75.8	38.0	0–74.5	36.2	82.5
Mid-banded**	0–86.2	29.0	2.8–87.3	37.9	60
Three-banded***	0–100	27.1	0–69.2	16.5	92
Light colored phenotypes together					
Y-0, Y-1, P-0, P-1	7.1–91.0	54.8	17.8–89.4	49.0	72

*The frequencies of brown unbanded shells (B-0) are not indicated, as they coincide with those of brown shells;**calculated from the number of banded shells; ***calculated from the number of multi-banded shells (i. e. shells with 3–5 bands); ****significant at p = 0.05. Other designations are similar to table 1. The small samples (IF-1, IF-2, L-4 and L-5 from Western Ukraine, M-6 and M-11 from the Moscow Region) were excluded from the calculations, see Material and methods.

lis from the Moscow Region, on average, yellow shells were found twice less often, but the mean frequency of pink mid-banded shells was four times higher (table 2).

Discussion

As we mentioned in previous publications (Gural-Sverlova & Egorov, 2021; Gural-Sverlova et al., 2020), in the regions we compare, as in other parts of Eastern Europe (Kolesnik & Kruglova, 2016; Mukhanov & Lisitsyn, 2018; Ostrovsky & Prokofieva, 2017), the phenotypic composition of *C. nemoralis* demonstrates a number of common features that can be interpreted as an accidental result of the transfer of a relatively small number of individuals (snails and/or their eggs) and the initial reduction of genetic and phenotypic diversity. This leads to the most frequent absence in the introduced populations of those traits, phenotypes or phenotype groups that are relatively rare or locally found even within the natural range, for example, a light lip, colorless (hyalozonate), light colored or "punctuate" bands, banded shells with brown ground color.

Among the phenotypes more common for *C. nemoralis*, which can reach rather high frequencies in certain parts of the natural range or in certain types of habitats, in the introduced Eastern European populations, brown unbanded and yellow unbanded shells are often absent or very rare, although in some cases they can even prevail. Among the main types of shell banding, in Eastern Europe, as in the natural range of *C. nemoralis* (Schilder & Schilder, 1957: table 13; Sverlova, 2002: table 3), shells with three lower bands are the least common.

However, not all features of the East European populations of *C. nemoralis* studied by various researchers can be explained by such stochastic population genetic factors as the founder effect or gene drift. Earlier, we suggested that the adaptation of introduced populations of this species to living in the more continental climate of Eastern Europe can lead, firstly, to an increase in the proportion of light-colored phenotypes, and secondly, to act against both the darkest (stronger) and the lightest (weaker) variants of shell coloration

(Sverlova, 2007). Both of these features were also observed in the introduced populations of the related species *C. hortensis* in Western Ukraine, which demonstrate not only an abnormally high proportion of unbanded shells increased even more recently, but also a clearly pronounced predominance among them of not the lightest (white), but yellow shells (Gural-Sverlova & Gural, 2018).

For *C. nemoralis*, both of these tendencies can be illustrated by comparing the ratio of different banding types among shells with different ground colors collected in Eastern Europe (our data) and in England (fig. 1), which is part of the natural range and has a relatively cool but mild maritime climate with smoothed temperature fluctuations. With a relatively similar ratio of yellow, pink, and brown shells in the considered sets, both in Western Ukraine and in Moscow Region, multi-banded shells are less common among pink ones, and in Western Ukraine — also among yellow shells. However, in both cases, a decrease in the overall intensity of shell coloration does occur not due to an increase in the proportion of the lightest phenotype (yellow unbanded, whose rare occurrence may be due to random factors, see above), and in the climatic condition of Moscow Region, more severe for *C. nemoralis*, also not due to yellow shells with one band (fig. 1). The predominant

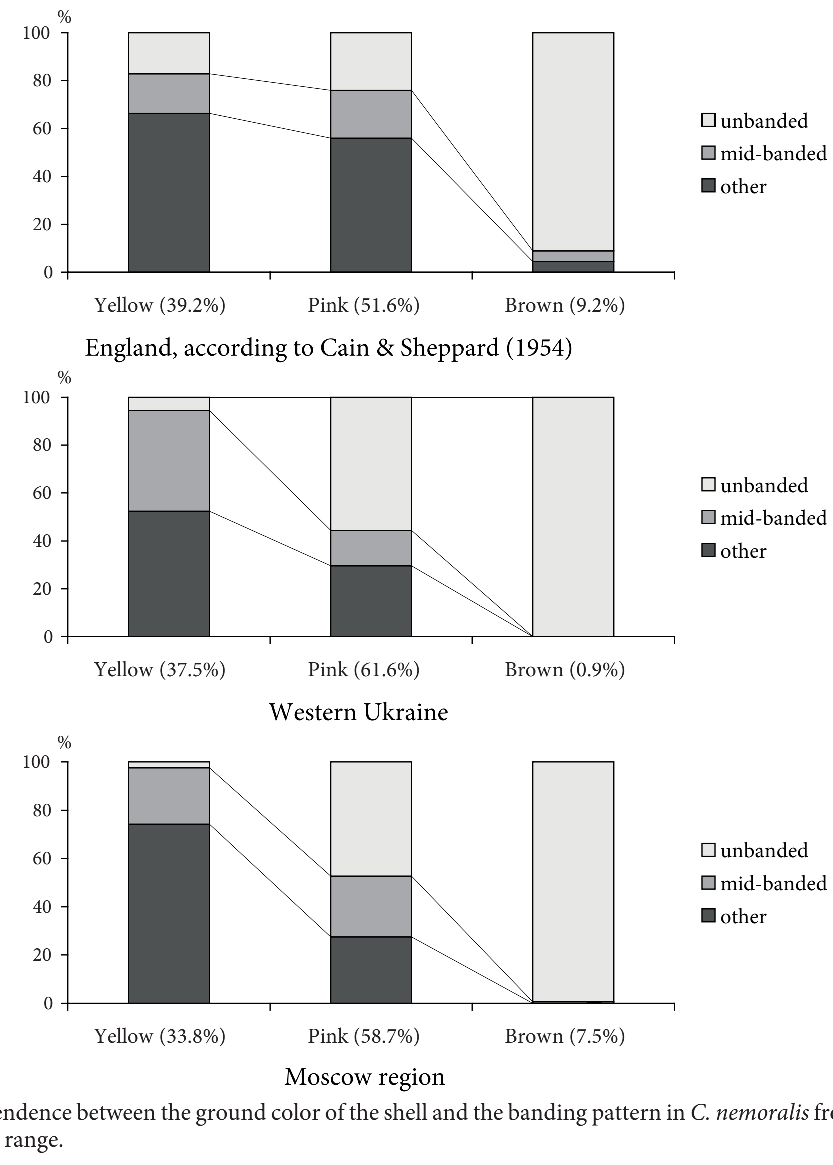

Fig. 1. Dependence between the ground color of the shell and the banding pattern in *C. nemoralis* from different parts of the range.

type of coloration in the introduced Eastern European populations of *C. nemoralis* often becomes an unbanded pink shell (tables 1, 3).

A number of facts have been described in the literature that indicate that lighter phenotypes in *Cepaea* are more resistant to not only extremely high, but also low temperatures, as well as to sharp fluctuations in ambient temperature (Arnason & Grant, 1976; Arnold, 1968; Lamotte, 1951, 1959). In particular, in most northern marginal populations of *C. hortensis*, snails with banded shells predominate (Alexandrov, Sergievsky, 1980; Arnason & Grant, 1976; Bengtson et al., 1979; Valovirta & Halkka, 1976 etc.). However, in Iceland, the relatively low (in general) frequency of unbanded individuals increases in the coldest habitats (Arnason & Grant, 1976). And in the north of Norway, where snails are forced to adapt to the most adverse climatic conditions, unbanded individuals predominate (Rost, 1952). A similar pattern was observed for *C. nemoralis* in the Pyrenees, when the frequencies of lighter — yellow and unbanded (Arnold, 1968), unbanded (Lamotte, 1951) — shells decreased at medium altitudes and increased again at high altitudes.

This is in good agreement with the physical properties of dark-colored shells, which should not only heat up faster, but also cool faster when the ambient temperature drops sharply (Arnason & Grant, 1976; Sverlova, 2004 a). Therefore, it has been suggested that lighter morphs may receive a selective advantage in a more continental climate, to which introduced populations of *C. nemoralis* are often forced to adapt (Sverlova, 2007). The formation of darker shells in *Cepaea* can occur in two ways: due to a darker ground color or the presence of the dark spiral bands. However, the pink unbanded or mid-banded shells remain lighter overall than yellow shells with 3–5 broad and almost black bands.

An analysis of the data published for introduced populations of *C. nemoralis* from different countries (table 3) shows that many of them, indeed, have a relatively high frequency of one or two of the light phenotypes, what will be described in more detail below. Although the set of predominant morphs in introduced populations can be very different (which is a completely natural consequence of the founder effect and subsequent stochastic population genetic processes), the total frequency of the 4 lightere variats of shell coloration in many cases exceeds 50 % (table 3). The average values of this indicator, calculated on the basis of a number of literature data for areas within the natural range of *C. nemoralis*, often turn out to be lower, although there are some exceptions, which are shown in table 3.

Particularly indicative in this respect is the high proportion of yellow unbanded shells in the cities of New York (Landman, 1956) and Marion (Clench, 1930; Johnson, 1927), eastern United States (table 3). In the city of Marion, the predominance of this phenotype was accompanied by a high proportion of yellow mid-banded shells. Compared to the related species *C. hortensis*, yellow unbanded shells are relatively rare in many populations of *C. nemoralis* within its natural range (Sverlova, 2007), although they reach higher frequencies in certain areas or in certain (open, with high insolation) habitats (table 3). In the American city of Burlington (New Jersey), where *C. nemoralis* was specially introduced from England in 1857 and multiplied in large numbers already by 1869, the prevailing coloration variant, as in many Eastern European populations of this species (see above), became a pink unbanded shell (Alexander, 1952).

Among the populations of *C. nemoralis* from the eastern United States presented in table 3, the general trend is violated by those from Lexington and Lynchburg, with a distinct predominance of five-banded phenotypes. This may be due to the founder effect: it is considered that mollusks were brought to Lynchburg by people from nearby Lexington (Richards, Murray, 1975), and to Lexington they were accidentally introduced from Italy or the British Isles already in 1883 (Howe, 1898). According to the monograph of Schilder & Schilder (1957: 180, map 72), snails with five-banded shells, on average, are more common on the northern and southern borders of the natural range of *C. nemoralis* than in its central part, which theoretically should increase the likelihood of their presence among the founding individuals.

Table 3. Peculiarities of the phenotypic composition of *C. nemoralis* from different parts of its range

Territory, source	N	Frequencies, %							
		grund color			light phenotypes				
		yellow	pink	brown	Y-0	Y-1	P-0	P-1	Total
Territories that are or may be part of the natural range									
Great Britain									
England, Warwickshire, Feldon area (Cameron & Pannet, 1985)	2746	42.9	55.6	1.4	3.7	6.8	9.3	11.4	31.2
England, Somerset, Berrow, dunes (Clarke & Murray, 1962; Murray & Clarke, 1978)	18 273	75.6	18.4	6.0	0.1	9.6	0.1	1.7	11.5
England, Berkshire Downs (Carter, 1968)	17 800	58.4	34.7	6.9	5.6	19.3	7.3	8.3	40.5
England, Berkshire, Lambourn Downs (Cain & Currey, 1963)	2795	63.6	32.3	4.1	12.0	43.1	7.9	19.8	**82.8**
England, Wiltshire, Marlborough Downs (Cain & Currey, 1963; Cowie & Jones, 1998)	7542	48.5	22.8	28.7	14.7	20.6	11.2	6.8	53.3
England, Wiltshire, Salisbury Plain (Cameron & Dillon, 1984)	1161	31.3	57.5	11.1	2.0	7.9	15.0	23.2	48.1
England, East Sussex, eastern South Downs (Arnold, 1971)	4725	71.6	28.2	0.2	4.5	12.8	0.9	3.6	21.8
England, Dorset, Purbeck Hills (Carter, 1968)	1538	67.8	17.0	15.1	4.8	15.3	1.0	5.8	26.9
England, Dorset, South Haven Peninsula (Cameron, 2001)	3954	1.6	98.1	0.3	0.1	1.3	0.8	37.6	39.8
England, Cornwall, Isles of Scilly (Murray, 1966)	4894	19.9	80.1	–	5.6	6.9	22.0	30.6	**65.2**
Great Britain, by habitat character (Cain & Sheppard, 1954)									
Beechwoods	2271	10.9	76.2	12.9	2.5	5.6	28.1	25.4	**61.7**
Other deciduous woods	5639	24.8	64.7	10.5	4.1	4.3	15.8	11.7	35.2
Hedgerows	3454	57.8	38.3	4.0	7.2	7.1	4.5	4.7	23.6
Rough herbage	3378	66.8	30.2	3.0	10.1	9.4	4.5	4.0	27.9
Short turf	1977	33.3	46.1	20.6	12.4	7.5	12.4	11.2	43.6
Great Britain and Ireland									
British and Irish coasts, dunes (Cain, 1968)	19 338	57.8	36.0	6.2	3.9	9.7	2.2	4.5	20.3
Ireland									
Donegal, dunes (Clarke et al., 1968)	23 857	33.0	?	?	8.9	0.4	5.2	≤1.0	≤ 15.5
Netherlands									
Groningen (Wolda, 1969 a)	4666	52.3	46.0	1.7	0.1	12.6	10.1	6.0	28.8
Gelderland (Wolda, 1969 b)	26 230	83.4	16.6	–	55.0	0.2	13.2	0.01	**68.4**
Germany									
*Northward from Thuringia and Saxony	8438	45.6	?	?	?	?	?	?	< 48.7
*Thuringia and Saxony	14 255	59.6	?	?	?	?	?	?	< 49.4
France									
Loir-et-Cher (Arnold, 1970)	1056	49.9	48.0	2.1	9.4	16.6	4.7	18.9	49.6
For the whole country (Lamotte, 1959)	152 305	?	?	?	?	?	?	?	< 49.1
France, Spain and Andorra									
Pyrenees (Arnold, 1968)	8806	81.9	18.1	–	33.6	2.3	4.7	0.9	41.5
Spain									
Pyrenees (Ramos, 1984)	6900	68.7	28.4	2.9	41.6	4.2	8.4	2.4	**56.7**
**Iberian Mountains (Mazon et al., 1989)	5066	30.5	69.5	?	3.7	2.7	6.2	11.2	23.8
Central Spain (Ramos, 1985)	2048	51.7	47.6	0.6	5.6	1.7	3.7	1.9	13.0
Italy									
North part of the Adriatic coast (Sacchi, 1984)	1427	73.4	26.6	–	11.1	8.2	3.4	3.6	26.3
Territories for which the species was introduced from the second half of the 19th century and later									
USA									
Massachusetts, Marion town (Clench, 1930; Johnson, 1927)	2779	52.2	47.6	0.2	21.5	20.9	9.5	24.4	**76.4**
Ibidem (Brussard, 1975)	22	81.8	18.2	–	45.4	31.8	–	9.1	**86.4**
New York, New York City (Landman, 1956)	1402	90.9	9.1	–	51.6	3.7	7.9	0.9	**64.1**
New Jersey, Burlington town, data from 1893 to 2014 (Örstan & Cameron, 2015)	591	?	?	?	?	?	?	?	**91.0**
Ibidem, collected in 1908 (Örstan & Cameron, 2015)	89	41.6	58.4	–	2.2	29.2	58.4	–	89.9

Ibidem, collected in 2013 and 2014 (Örstan & Cameron, 2015)	12	58.3	41.7	–	–	50.0	33.3	8.3	**91.7**
Virginia, Lexington town (Howe, 1898)	3543	90.8	?	?	?	?	?	?	about 10
Ibidem (McConnell, 1936)	1553	96,9	3.1	–	29.7	10.0	1.4	1.1	42.2
Ibidem (Brussard, 1975)	315	96.8	3.2	–	36.8	2.8	0.6	0.3	40.6
Virginia, Lynchburg town (Brussard, 1975; Richards & Murray, 1975)	2761	100.0	–	–	15.5	2.9	–	–	18.5
***6 other localities (Brussard, 1975)	416	51.7	40.1	8.2	19.9	7.0	15.1	11.8	**53.8**
Czech Republic									
Bohemia (Honěk, 1995)	14 249	49.9	50.1	–	0.7	21.3	10.5	17.3	49.9
Poland									
Lower Silesian Voivodeship, around Wrocław City (Pokryszko et al., 2012)	9340	55.7	44.1	0.2	17.7	7.8	12.0	9.5	47.0
Subcarpathian Voivodeship, end of 19-th century (SMNH NANU)	46	58.7	41.3	–	2.2	30.4	–	17.4	50.0
Ibidem (Ożgo, 2005)	7307	72.6	27.4	<0.1	2.0	51.2	4.4	17.2	**74.8**
Ukraine									
Ivano-Frankivsk, Lviv and Ternopil Regions, 2019–2020 (this publication)	3736	37.5	61.6	0.9	2.1	15.7	34.3	9.1	**61.2**
Belarus									
Mogilyov Region, Bobruisk town (Ostrovsky & Prokofieva, 2017)	280	17.1	77.5	5.4	–	5.0	30.4	28.2	**63.6**
European part of Russia									
Moscow Region, 2006–2020 (this publication)	2112	33.7	58.7	7.5	0.8	7.9	27.7	14.8	**51.3**
Nizhny Novgorod Region, Nizhny Novgorod City, 3 colonies with unspecified size of each sample (Mukhanov & Lisitsyn, 2018)	218	47	53	–	–	47	13	40	**100**
		27	73	–	–	–	67	6	73
		100	–	–	–	100	–	–	**100**

*Calculated using modified data from the Schilder´s archive used in the article (Sverlova, 2004 b); **excluding rare brown shells not concretely mentioned in the article; ***total for 6 settlements in Virginia (Staunton, Warm Springs, Harrisonburg), Massachusetts (Brewster, Eastham) and New York (Brighton); ≤ — the real frequency may be slightly less than the specified value due to the lack of data on the full composition of the phenotypes; < in the last column — the indicated amount also includes the frequencies of dark phenotypes B00000 and B00300; ? — it is impossible to calculate according to the data available in the publication; SMNH NANU — collection of the State Museum of Natural History in Lviv. Locations within one country are mentioned from north to south (England, Netherlands, Germany, Spain, USA) or from west to east (Poland, Russia). Frequencies in the last column exceeding 50 % are shown in bold.

The proportion of unbanded shells in Lexington was about 4 % at the end of the 19th century, 14–15 years after the introduction (Howe, 1898). By 1930 (McConnell, 1936) it increased more than 7 times, which was caused by the increase in the proportion of the lightest phenotype (yellow unbanded). The total frequency of the 4 light phenotypes over the same period of time increased approximately 4 times (table 3). This may be an indication of strong climatic selection favoring snails with light-colored shells. It should also be noted that in Lexington, already at the very early stages of research, shells with weak, rudimentary, or split bands were often found (Howe, 1898), which could somewhat reduce the intensity of pigmentation of five-banded shells.

More than half of *C. nemoralis* individuals collected in the Subcarpathian Voivodeship of Poland in 1998–2000 (Ożgo, 2005), were represented by only one phenotype (yellow mid-banded). The malacological collection of the State Museum of Natural History in Lviv demonstrates that a high proportion of this morph was also characteristic during the initial stages of the introduction of *C. nemoralis* to southeastern Poland, when this species was first recorded in Łańcut (Bąkowski, 1880) and Rzeszów (Łomnicki, 1899). In the samples collected both at the end of the 19th century and the end of the 20th century, the proportion of the unbanded shells (not only yellow, but also pink) was very low (table 3). This may be attributed to the founder effect or random genetic drift in the initial stages of colony formation. Unfortunately, the samples from the end of the 19th century are too small to be able to analyze possible changes in the phenotype frequencies that could have occurred during the 20th century.

Such a pronounced predominance of one (or two) of the lightere phenotypes was not observed either in the Czech Republic (Honěk, 1995) or in southwestern Poland (Pokryszko et al., 2012), i. e. in regions less distant from the eastern and south-eastern boundaries of the natural range of *C. nemoralis* (Gural-Sverlova & Egorov, 2021). Although in the Czech Republic, the total frequence of yellow and pink mid-banded shells was also close to 40 %. In southwestern Poland, snails with unbanded shells were relatively more common. The total proportion of those with yellow and pink ground colors there was 30 %, with a slight prevailing of the lighter (yellow) phenotype. The total frequency of the 4 lightest phenotypes both in the Czech Republic and in the south-west of Poland also practically does not differ from the average values of this indicator in neighboring Germany (table 3). Therefore, it is possible that climatic selection in the territories adjacent to the natural range of the species is not so strong. At the same time, the chance of repeated introductions of snails and replenishment of the initial gene pool of the introduced populations here is higher.

An interesting experiment was conducted at the end of the 20th century in Prague (Honěk, Martinkova, 2003). In 1995, mature and large immature individuals of *C. nemoralis* from a single sample (N = 391) collected in the north-east of the Czech Republic were released at 9 sites. The most common in the sample were pink five-banded shells (25.8 %). Then, in decreasing order of frequencies, there were pink mid-banded (19.4 %), pink unbanded (16.9 %) and yellow mid-banded shells (16.4 %). Yellow unbanded shells were absent. Before release to the new sites, the snails were sorted by shell color and banding pattern. Observations in 1997–2003 showed that snails did not survive at 5 sites, including two sites where mollusks with pink or yellow five-banded shells were released. The initially released phenotype (pink or yellow mid-banded) was predominant at two sites. At another two sites, where pink individuals without bands or with three upper bands were released, the phenotype yellow mid-banded became predominant. The same phenotype also prevailed in a single colony, apparently formed due to the migration of snails from the site where individuals with pink unbanded shells were released. As a result, yellow mid-banded shells became predominant in the formed colonies of *C. nemoralis*, their share was 65.8 % of all individuals found.

Conclusions

In different parts of Eastern Europe, a number of similar features of the phenotypic composition of *C. nemoralis* are observed, which can only partly be explained by the greater likelihood of the founding individuals having traits that are more common in the natural range of this species. Both in Eastern Europe and in other introduced populations of *C. nemoralis*, there is often a well pronounced predominance of one or two of the 4 lightere variants of shell coloration (yellow unbanded, yellow mid-banded, pink unbanded or pink mid-banded), which, probably, can be interpreted as the result of the adaptation to the more continental climate conditions compared to the natural part of the present range of this species. However, since the studied Eastern European populations of *C. nemoralis* are still relatively young (Egorov, 2018; Gural-Sverlova et al., 2020), a more reasoned answer to this question requires a study of the long-term dynamics of their phenotipic composition.

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