

Distribution and shell colour and banding polymorphism of the *Cepaea* species in Bohemia (Gastropoda: Helicidae)

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Abstract. The distribution of the local populations of *Cepaea hortensis* (Müller), *C. nemoralis* (Linnaeus), and *C. vindobonensis* (Férussac) in Bohemia and frequency of colour and shell banding morphs were recorded in 1987 - 1994. The species differ in their habitat preferences and geographic distribution. While *C. hortensis* occurs at both urban and country localities over the whole Bohemia, *C. nemoralis* is limited to urban localities of northern, central and eastern Bohemia and *C. vindobonensis* lives at steppe localities along the Labe river and its major tributaries, and in the Central Bohemian Karst. The frequency of pink morph in local populations of both species varied between 0 and 100 percent and was higher in *C. nemoralis* than *C. hortensis* populations. In both species the distribution of populations with high frequency of yellow or pink morphs is mosaic, and the same mosaic pattern has distribution of 00000 and 12345 morphs. High frequency of shell banding morphs 00300 and 00345 in *C. nemoralis* is limited to small areas. In both species there was no relationship between the above sea level altitude of the locality and percentage of pink or melanic individuals in local populations. *C. vindobonensis* populations of Bohemia show little variation.

INTRODUCTION

The presence of three *Cepaea* species, *C. hortensis* (Müller), *C. nemoralis* (Linnaeus), and *C. vindobonensis* (Férussac) in Bohemia was established since the beginnings of a scientific interest in malacology. The results of earlier works were summarized by Ložek (1956) who reviews several papers concerning the *Cepaea* species (e.g. Slavík 1865, Petrbock 1943, Sobotka 1945). Later on, distribution and variation in *Cepaea* species were not studied in detail except the work of Schilder & Schilder (1957) which marginally concerns the territory of Bohemia. Some results were published from surrounding areas of Central and Southern Europe (Jones 1973b, Rafiński 1981).

Earlier studies revealed the differences in geographic distribution of Bohemian *Cepaea* species. While *C. hortensis* populations were found at the whole territory other species were limited to some areas. *C. nemoralis* was found only in the north of the country and in several towns of western and central Bohemia (Karlovy Vary, Litoměřice, Nový Bydžov), and *C. vindobonensis* was limited to lowland surroundings of the river Labe and its major tributaries, and the karst areas of central Bohemia. The authors also mentioned typical differences in species requirements for habitat quality. Although the occurrence of colour and shell banding morphs was well documented, a systematic study of their frequencies in local populations was not undertaken. Honěk (1995) studied local distribution and shell colour and banding polymorphism of *C. nemoralis*. This work revised earlier results and presented some speculations on the causes of local differences in distribution patterns of *C. nemoralis* and *C. hortensis*.

The aim of this paper is to present a summary of distribution and variation of *C. hortensis* and publish the data on morph frequencies in local populations of *C. hortensis* and *C. nemoralis*. These data could provide a basis for the study of temporal changes in geographic distribution and polymorphism which may take an important part in determining the patterns of local morph variation (cf. Currey et al. 1968, Wall et al. 1980). Habitat preferences of the species are also discussed.

MATERIAL AND METHODS

Cepaea nemoralis and *C. hortensis* were collected systematically at the whole territory of Bohemia, in 1987-1994. Northern Bohemia was investigated with a particular intensity due to simultaneous occurrence of both species. On many localities brief visits enabled only investigating the most convenient habitats - roadsides, shrubs, urban ruderal areas and cemeteries (the latter were particularly convenient for all *Cepaea* species). The above sea level altitude of the localities was read from 1:50,000 maps. The geographic position of the localities (Appendices I and II) is indicated with respect to a reference grid used for faunistic mapping of the country (Novák 1989) which is identical with the one used for floristic research in Central Europe (Slavík 1971). The surface of the country is divided into rectangles. Their west-east dimension is 10' geographic longitude and north-south dimension is 6' geographic latitude (approximately 11 x 12 km). The rectangles are designated in the west-east (longitudinal) direction by serial numbers beginning with 38 (easterly of 12°00' E), and in the north-south (latitudinal) direction by serial numbers beginning with 49 (southerly of 51°06' N). Each rectangle is indicated by an apposition of its longitudinal and latitudinal serial number.

The colour and shell banding forms were scored in adult living animals and well preserved dead shells. The localities where >10 *C. nemoralis* or >20 *C. hortensis* individuals were collected were considered for statistic evaluation. The difference was made due to importance of *C. nemoralis* data from marginal populations. These data are included in the Appendices 1 and 2. The colour of the shells was classified as "yellow" or "pink". In several populations the colour of some individuals was so pale that distinguishing of yellow and pink forms was difficult. In this case individuals with a trace of the pink colouration (usually near the top of the shell) were classified as "pink", the rest was classified as "yellow". The shell banding morphs were classified according to generally accepted conventions. The bands are designated as 1 to 5 beginning from the dorsal side, and a fusion of bands was indicated by brackets. As the number of fused bands could increase with animal age the number of fusions was counted at 1/4 whorl from the shell outlet. The duplicated bands (rare) were censused as single ones. "Hyalozonate" individuals whose bands were replaced by pale blanks (frequent in some *C. hortensis* populations) and individuals whose bands were diffuse (lacking the sharp edges) were censused as corresponding banded morphs. In total, 417 populations of *C. hortensis* at 343 geographic localities, 220 populations of *C. nemoralis* at 136 localities, and 35 populations of *C. vindobinensis* were sampled.

RESULTS

1. Habitats

In Bohemia, all *Cepaea* species live at urban sites as well as at country habitats little affected by human activity. The populations were most often encountered at (1) urban habitats - street margins, parks etc., (2) cemeteries and (3) country habitats - grassy stands, shrubs, hedgerows, roadsides and other structures created by human activity.

Typical preferences of the *Cepaea* species differ largely. The main differences were (1) tendency to colonize urban or country habitats, (2) the type of vegetation cover, and (3) the altitude of the locality (Fig. 1).

C. hortensis is most tolerant in its requirements for habitat quality. The species lives at habitats grown by broad leaved and grassy herbs, as well as in the understory of shrubs. It was encountered at both urban (61 % of cases) and country (39 %) localities (cemeteries were not included). The species was distributed evenly from lowland (160 m a.s.l.) to submontane (740 m a.s.l.) areas.

C. nemoralis inhabits mostly localities grown by broad-leaved weedy stands and understory of shrubs. It occurs scarcely at places grown by grassy vegetation. Most localities were within urban areas and only a small fraction (1 %) were the roadsides in the near surroundings of the towns.

Tab1 Graf 1

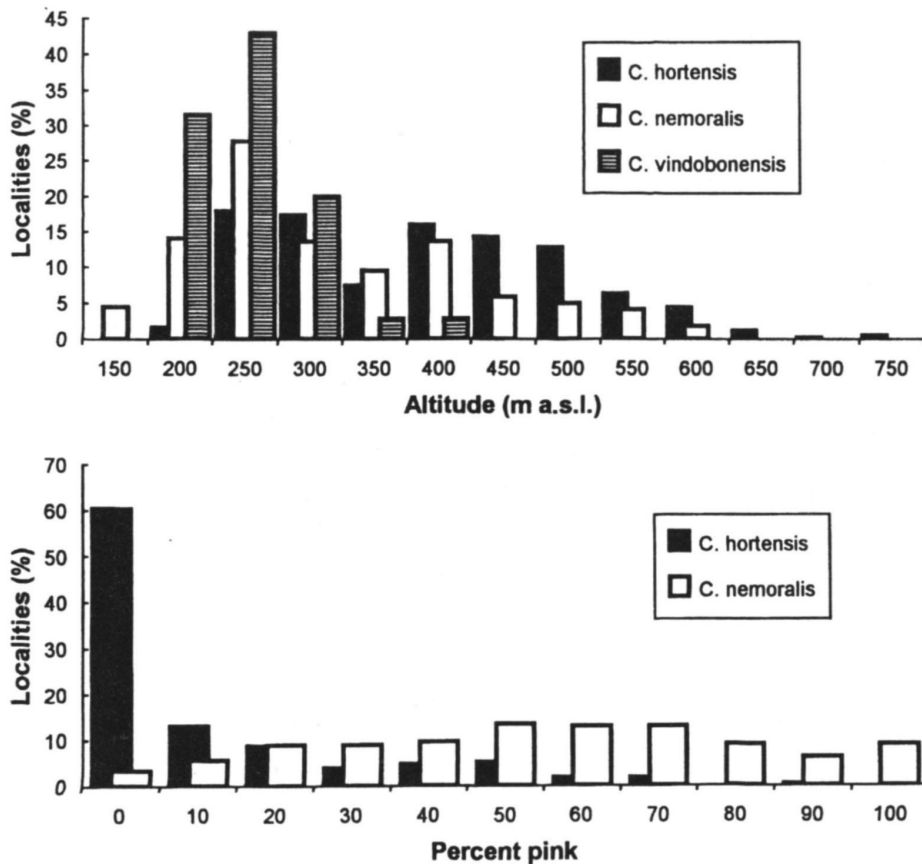


Fig. 1. Above: Altitudinal distribution of Bohemian localities of the *Cepaea* species. Below: Frequency of *C. hortensis* and *C. nemoralis* populations according to the percentage of the pink form.

The populations were found over a wide altitudinal range (140 - 580 m a.s.l.), mostly below 450 m a.s.l.

C. vindobonensis lives at grassy steppe localities and at ruderal areas grown by mixed dycotyledonous and grass stands. Most localities were in the country (93 %). The species was found at lowland localities between 170 and 400 m a.s.l.

2. Geographic distribution

The three *Cepaea* species in Bohemia differ in their patterns of geographic distribution. Populations of *C. hortensis* were found, with notable exceptions, over the whole territory (Fig. 2). They were absent in montane areas bordering Bohemian frontiers - Novohradské hory, Šumava, Český les, Lužické hory, Jizerské hory, Krkonoše, Broumovské stěny and Orlické hory Mountains. The populations were apparently absent (or very scarce) also at some areas of 400 - 700 m a.s.l. altitude. This concerns the northwest of the country - Džbán, České Středohoří and Labské pískovce Hills, and Slánská tabule and Podkrušnohorská pánev Plains. An area where *C. hortensis* populations were also not found is the Brdy Mountains, the north of Plzeňská pahorkatina Hills, and Tepelské vrchy, Doupovské vrchy and Slavkovský les Mountains. *C. hortensis* populations are also less frequent in the areas where this species is replaced (at some localities) by *C. vindobonensis* and *C. nemoralis*.

C. nemoralis populations (Fig. 2) were found in northern Bohemia. The areas where they occupied the majority of the convenient urban sites were (a) the north of the country (bordered by Labské pískovce, Česká středohoří, Polomené hory, Ralsko-bezdězská tabule, Český ráj, and Jizerské hory Mountains), and the towns of (b) Litoměřice and (c) Nový Bydžov with their near

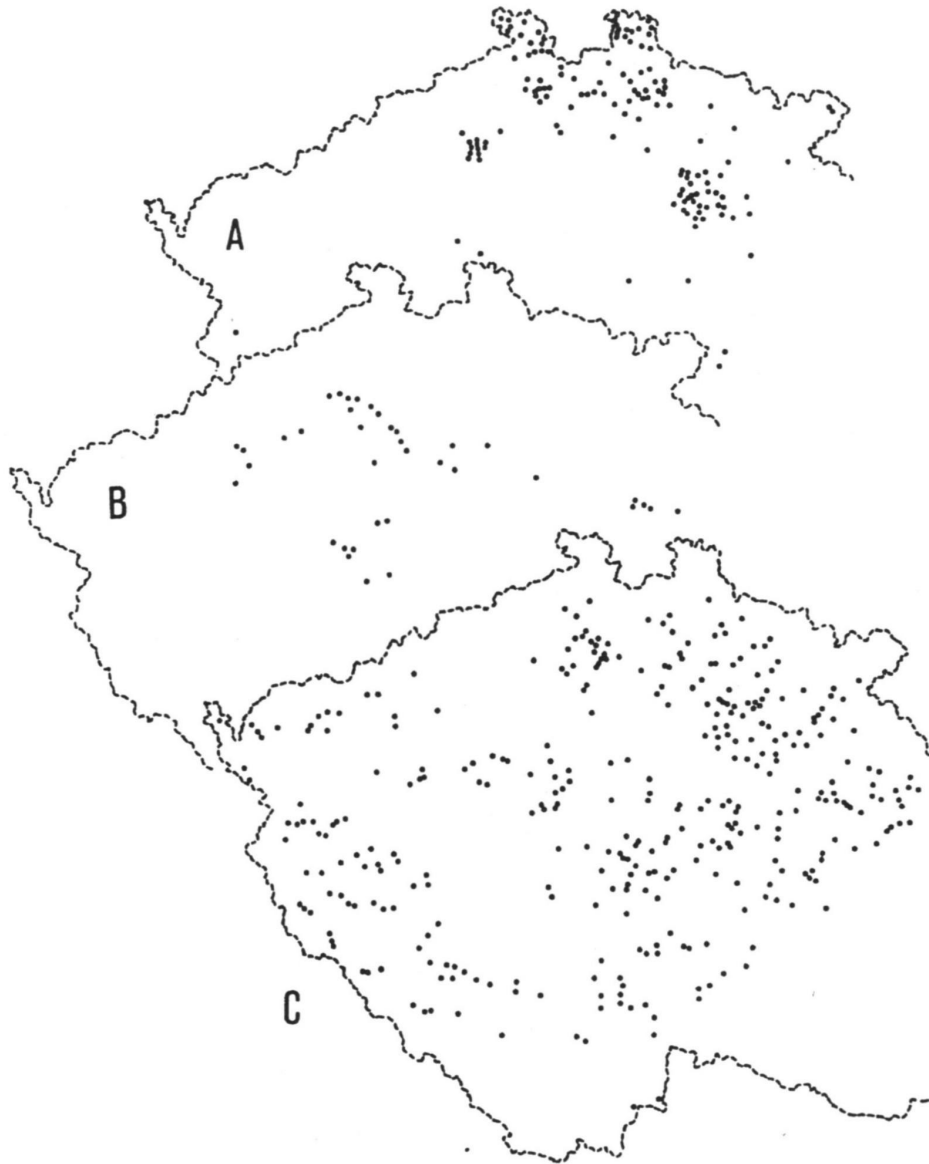


Fig. 2. Geographic distribution of (A) *C. nemoralis*, (B) *C. vindobonensis*, and (C) *C. hortensis* populations.

surroundings. In between these areas, *C. nemoralis* populations occurred at some urban localities but other ones were populated by *C. hortensis*. More southerly only few isolated populations were found, in Tachov (western Bohemia), Tuchlovice, Unhošť and Zásmyky (central Bohemia) and Chotusice, Havlíčkův Brod and Dolní Krupá (eastern Bohemia). The latter localities should be added to the list published by Honěk (1995).

C. vindobonensis was distributed at lowland localities of central Bohemia, along the Labe river and its major tributaries, Jizera, Vltava and Ohře, and in the Středočeský kras karst area of central Bohemia. Several occasionally recorded localities are shown in Fig. 2.

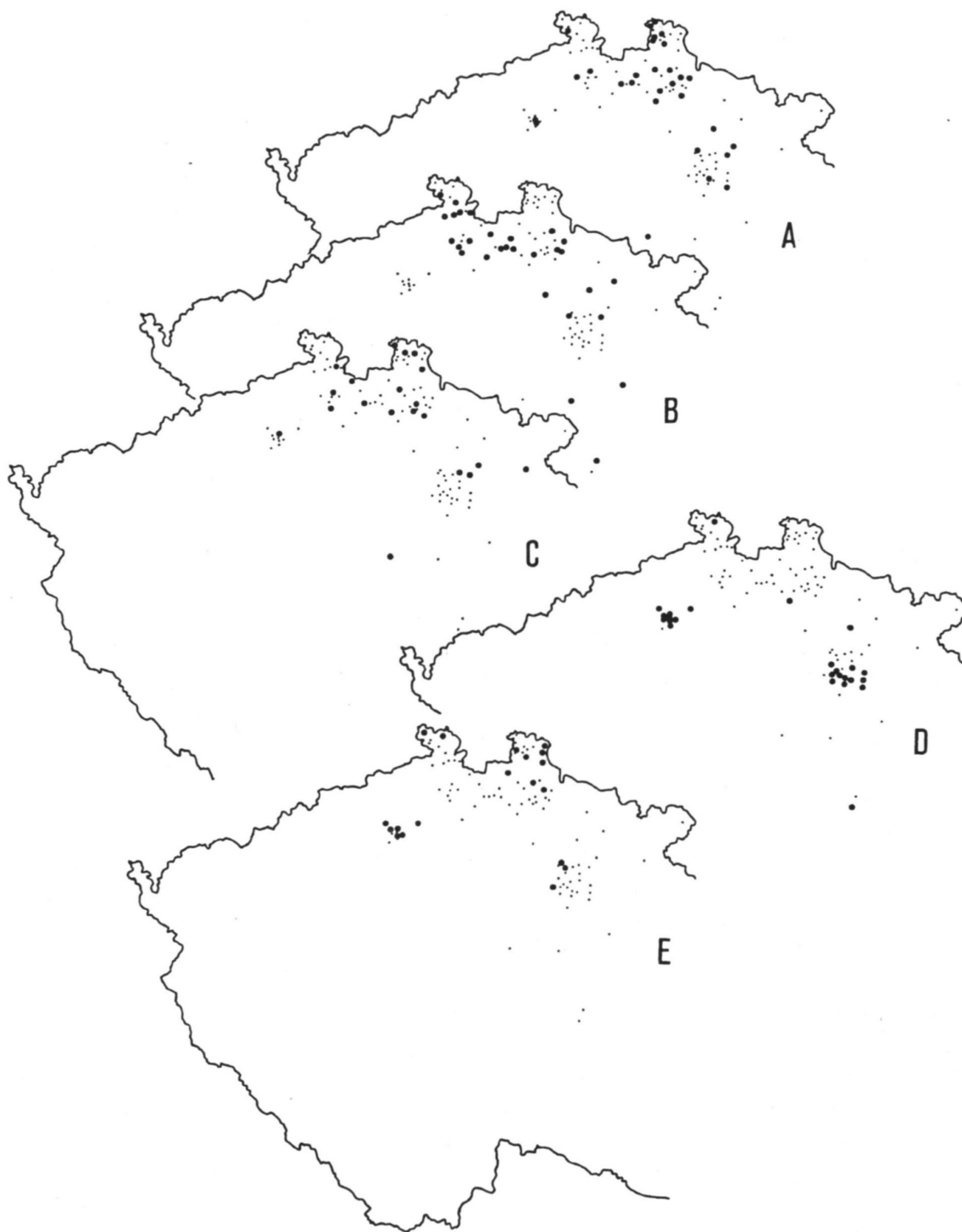


Fig. 3. Geographic distribution of *C. nemoralis* populations with high proportions of colour and shell banding forms. The large points represent populations with (A) >80% of pink individuals, (B) >90% of 12345 individuals, (C) >30% of 00000 individuals, (D) >50% of 00300 individuals, and (E) >5% of 00345 individuals. The small points represent other localities where >10 individuals of *C. nemoralis* were collected.

3. Frequency of shell colour and banding forms in local populations

Bohemian populations of *C. vindobonensis* are practically monomorphic. The only variation is a reduction of the bands 1 and 2, and occurrence of hyalozonate individuals (Ložek 1956). Only few individuals showing this type of variation were found. The variation of *C. nemoralis* and *C. hortensis* is discussed below.

3.1 Shell colour

Both *C. hortensis* and *C. nemoralis* have either a yellow or a pink shell colour. The populations with an increased percentage of the pink form were more frequent in *C. nemoralis* than *C. hortensis* (Fig. 1). In *C. nemoralis* there was no trend to local aggregation of populations with a high frequency of the pink morph (Fig. 3). In fact, the range of variation in the frequency of pink form was similar in 53 populations collected on a small area of the towns of Litoměřice and Nový Bydžov (ca 20 km²), and the 125 populations from the rest of the country. *C. hortensis* populations with a high frequency of pink form were also scattered over the whole country (Fig. 4) and interspersed with populations containing small percentage of pink individuals.

3.2 Shell banding

Populations of *C. hortensis* consisted of bandless 00000 or five banded 12345 individuals. In local populations the morphs were present in proportions ranging from 0 to 100 %. Populations consisting of >90 % unbanded individuals were aggregated in the eastern part of the country (Fig. 4) while populations consisting only of 12345 individuals were found more frequently in the west (Fig. 4). However, these populations were interspersed with populations containing intermediate proportions of both forms. Many *C. hortensis* populations contained banded individuals with two or more confluent bands. The distribution of populations with a high frequency of individuals with fused bands was mosaic.

Populations of *C. nemoralis* contained shell banding morphs 00000, 00300, 00345, and 12345 whose distribution was discussed in detail by Honěk (1995). The populations with a high percentage of morphs 00000 and 12345 (Fig. 3) were scattered over the whole area of species' geographic distribution while the ones with a high frequency of 00345 and 00300 morphs were aggregated (Fig. 3). The distribution of the latter morphs may be considered as an example of area effects. The populations with high proportions of individuals with band fusions were scattered evenly over the whole territory.

4. Morph frequency and the altitude of the locality

We investigated the relationship between the above sea level altitude of the locality (which is a correlate of climatic conditions) and proportion of morphs which might have a thermoregulatory function. There was no correlation between the altitude of the locality and the percentage of pink individuals, or the percentage of pooled melanic (123)(45) and (12345) morphs in the respective populations.

DISCUSSION

In Western Europe, the intraspecific variation of shell colour and banding patterns in *Cepaea* species was studied by many authors, since the late 19th century. The materials were sampled at

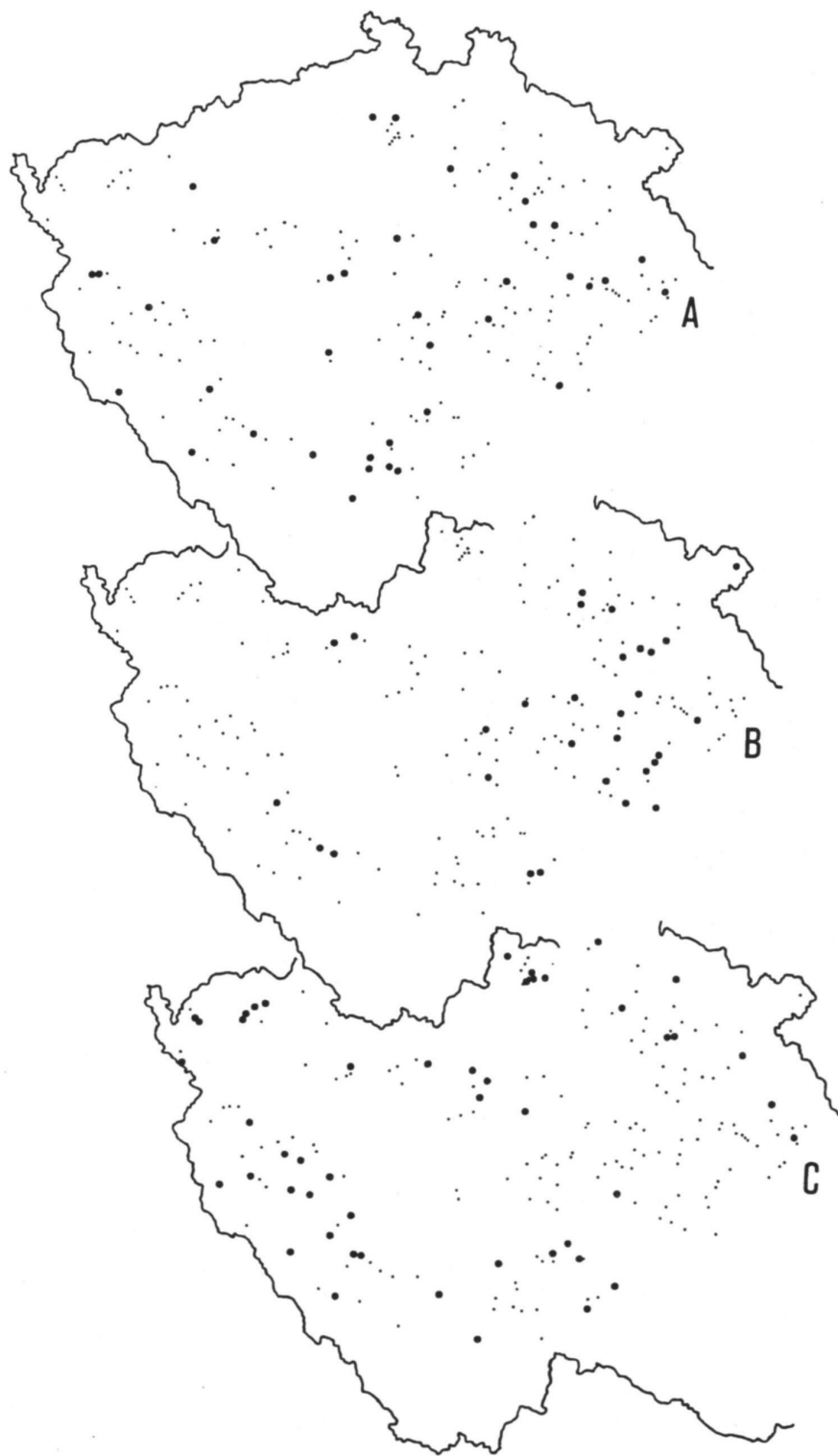


Fig. 4. Geographic distribution of *C. hortensis* populations with high proportions of colour and shell banding morphs. The large points represent populations with (A) >20% of pink individuals, (B) >90 % of 00000 individuals, and (C) 100% of 12345 individuals. The small points represent other localities where >20 individuals of *C. hortensis* were collected.

a vast number of localities, particularly in Britain, Spain, France and Germany. The local variation in morph frequency was related to climatic and microclimatic factors (Jones & Irving 1975, Ramos 1984, 1985, Ratel et al. 1989, Khemici et al. 1989), visual selection by avian predators (Cain & Sheppard 1954, Cain 1968) and historical events including founder effects (e.g. Lamotte et al. 1988) which modify the action of selective forces. Despite the large body of accumulated knowledge the problem resisted the conclusive solution (Jones 1973a, Jones et al. 1977, Cain 1983, Lamotte 1988). Comparative studies of morph frequencies in local populations continue in contributing relevant information for the study of *Cepaea* polymorphism. This study presents results from Bohemia, a territory rather isolated by surrounding mountains and spatially separated from Western Europe, with continental climatic conditions.

There exist several analogies as well as important differences between Bohemian and West-European populations of *C. nemoralis* and *C. hortensis*:

(1) The geographic area of *C. nemoralis* distribution is smaller than the one of *C. hortensis* (cf. Ložek 1956, Jones & Clarke 1969, Ramos 1985). In the centre of the overlap of geographic areas of both species, the oceanic area of Western Europe, both species occupy similar urban and country habitats and frequently occur in mixed populations (Schilder & Schilder 1953, Mazon et al. 1989). Habitat preferences of both species in Bohemia are different. *C. nemoralis* occupies urban sites. *C. hortensis* lives in the country habitats as well as at urban sites. The latter are occupied by *C. hortensis* in absence of *C. nemoralis*. Otherwise *C. nemoralis* replaces *C. hortensis* at urban sites almost completely and both species rarely occur in mixed populations (Honěk 1995). Similar differentiation of habitat preferences was observed also in Poland (Rafiński 1981). Our results indicate also different altitudinal preferences. *C. hortensis* occupied many localities at altitudes of >300 m a.s.l. where *C. nemoralis* populations were less frequent. However, this "tolerance" to highland conditions could be a consequence of the limited geographic distribution of *C. nemoralis*. *C. hortensis* inhabits highland areas of Českomoravská vrchovina and submontane areas of western and southern Bohemia where *C. nemoralis* is absent. Climatic differences between lowland and highland areas are small, not likely to limit the presence of *C. nemoralis* although this species is probably less tolerant to harsh conditions than *C. hortensis* (cf. Jones & Clarke 1969).

(2) *Cepaea hortensis* and *C. nemoralis* differ in overall proportion of shell colour morphs. The average proportions are in accordance with continental trends. In *C. nemoralis* the average frequency of pink morph is in between the Mediterranean populations with a high frequency of yellow morph and Atlantic populations with increased frequency of pink form (Lamotte 1988). The overall proportions in Bohemian populations may be affected by continental climate with average temperatures lower than in the Mediterranean region and scarce rainfalls. Local effects of climatic selection (Jones & Irving 1975, Ramos 1984, Lamotte et al. 1988, Khemici et al. 1989) could not be detected. The average frequency of pink form in *C. hortensis* populations is lower than in *C. nemoralis*. This situation is similar to Western Europe, France (Guerrucci 1974), Britain (Cain et al. 1969) and Germany (Schilder & Schilder 1953).

(3) Differences were found also in occurrence of shell banding morphs. Common morphs of *C. nemoralis* present in Western Europe, 00000, 00300, 00345, and 12345 were found also in Bohemia. By contrast, only two morphs of *C. hortensis*, 00000 and 12345, occur in Bohemia, in contrast to French populations where also 00300, 10305, and 00345 morphs were found (Guerrucci 1974). Similar constraints on variation, however, were found in British (Cain et al. 1969) and German (Schilder & Schilder 1953) populations of *C. hortensis*.

(4) Patterns of variation between local populations of *Cepaea* in Bohemia and Western Europe are similar in that frequencies of shell colour and banding morphs vary largely between populations separated by a small distance or even across a population continuum (Wolda 1969). As a result, the distribution of populations with different frequencies of particular morphs is

usually mosaic. Area effects, occurrence of a high proportion of a morph in several populations aggregated in an ecologically heterogeneous area, were established in West European populations of *C. nemoralis* (Cain & Currey 1963). It was suggested that their existence is associated with unstable habitats and their origin favoured by "historical" events (founder effect) rather than by the selection process (Cameron et al. 1984, Cameron & Dillon 1984). The existence of area effects in Bohemian populations of *C. nemoralis* is an interesting exception. The localities with a high frequency of 00300 and 00045 morph are aggregated on a rather large area. I suppose that the area effects are a consequence of the founder effect during the recent expansion of this species in northern Bohemia (Honěk 1995). In contrast to *C. nemoralis*, no trace of area effects was found in *C. hortensis* whose populations are long established in this area.

In this work only a marginal interest was paid to *C. vindobonensis*. It is a pontic species which inhabits south-eastern and eastern-central Europe. Czech Republic is near the north-west edge of its geographic distribution (Ložek 1956). The absence of variation in many Bohemian populations contrasts with southern populations where hyalozonate individuals may be rather frequent (Jones 1973a, 1974). The difference is probably due to lower intensity of thermal stress in Bohemian populations.

Compared with earlier results (Ložek 1956), our data confirmed the statements on habitat preferences of the *Cepaea* species, and indicated the spreading of the area of geographic distribution of *C. nemoralis* (Honěk 1995). Curious is the present absence of this species at the territory of Prague (Juříčková 1994). This is a cross-road of traffic and offers many sites convenient for *C. nemoralis*.

A c k n o w l e d g e m e n t

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REFERENCES

- CAIN A. J. 1968: Studies on *Cepaea*. V. Sand-dune populations of *Cepaea nemoralis* (L.). *Phil. Trans. Roy. Soc. London, B* **263**: 499-647.
- CAIN A. J. 1983: Ecology and ecogenetics of terrestrial molluscan populations. pp: 597-647. In: Russell-Hunter W.D. (eds.): *The Mollusca*. Vol. 6. Ecology. London, New York, San Francisco: Academic Press, pp.
- CAIN A. J., CAMERON R. A. D. & PARKIN D. T. 1969: Ecology and variation of some helicid snails in northern Scotland. *Proc. Malacol. Soc. Lond.* **38**: 269-299.
- CAIN A. J. & CURREY J. D. 1963: Area effects in *Cepaea* on the Larkhill Artillery Ranges, Salisbury Plain. *J. Linn. Soc. (Zool.)* **45**: 1-15.
- CAIN A. J. & SHEPPARD P. M. 1954: Natural selection in *Cepaea*. *Genetics* **39**: 89-116.
- CAMERON R. A. D., CARTER M. A. & PALLES-CLARK M. A. 1980: *Cepaea* on Salisbury Plain: patterns of variation, landscape history and habitat stability. *Biol. J. Linn. Soc.* **14**: 335-358.
- CAMERON R. A. D. & DILLON P. J. 1984: Habitat stability, population histories and patterns of variation in *Cepaea*. *Malacol.* **25**: 271-290.
- CURREY J. D. & CAIN A. J. 1968: Studies on *Cepaea*. IV. Climate and selection of banding morphs in *Cepaea* from the climatic optimum to the present day. *Phil. Trans. Roy. Soc. London, B* **253**: 483-489.
- GUERRUCCI M. A. 1974: Le polymorphisme de la coquille chez *Cepaea hortensis* Muller (Mollusques, Pulmonés) en France. *Mém. Soc. Zool. Fr.* **37**: 103-127.
- HONĚK A. 1995: Geographic distribution and shell colour and banding polymorphism in marginal populations of *Cepaea nemoralis* (Gastropoda, Helicidae). *Malacologia* **37**: 111-122.
- JONES J. S. 1973a: Ecological genetics and natural selection in molluscs. *Science* **182**: 546-552.
- JONES J. S. 1973b: The genetic structure of a southern peripheral population of the land snail *Cepaea nemoralis*. *Proc. Roy. Soc. London, B* **183**: 371-384.

- JONES J. S. 1974: Environmental selection in the snail *Cepaea vindobonensis* in the Lika area of Yugoslavia. *Heredity* **32**: 165-170.
- JONES J. S. & CLARKE B. A. 1969: The distribution of *Cepaea* in Scotland. *J. Conchol.* **27**: 3-8.
- JONES J. S. & IRVING A. J. 1975: Gene frequencies, genetic background and environment in Pyrenean populations of *Cepaea nemoralis* (L.). *Biol. J. Linn. Soc.* **7**: 249-259.
- JONES J. S., LEITH B. H. & RAWLINGS P. 1977: Polymorphism in *Cepaea*: a problem with too many solutions? *Annu. Rev. Ecol. Syst.* **8**: 9-143.
- JUŘIČKOVÁ L. 1994: [Molluscs of Velká Praha and their evolution]. *Živa* **62**: 78-79 (in Czech).
- KHEMICI E., GÉNÉRMONT J. & LAMOTTE M. 1989: Relation entre polymorphisme et milieu chez les *Cepaea nemoralis* (Mollusques Pulmonés) de Normandie. *Bull. Soc. Zool. Fr.* **113**: 155-167.
- LAMOTTE M. 1988: Facteurs influençant la diversité du polymorphisme de la coquille dans les populations naturelles de *Cepaea nemoralis* (Moll. Pulmonés). *Haliotis* **18**: 131-157.
- LAMOTTE M., KASSEM I. & GÉNÉRMONT J. 1989: Le polymorphisme de la coquille de *Cepaea nemoralis* (L.) dans la Vallée d'Ossau (Pyénées Françaises). *Bull. Soc. Zool. Fr.* **113**: 53-63.
- LOŽEK V. 1956: [Key of Czechoslovak Mollusca]. Bratislava: Vydavateľstvo Slovenskej Akademie Vied, 359 pp (in Czech).
- MAZON L. I., MARTINEZ DE PANCORBO M. A., VICARIO A., AGUIRRE A. I., ESTOMBA A. & LOSTAO C. M. 1989: Selection in sympatric populations of *Cepaea*. *Genet. Sel. Evol.* **21**: 269-281.
- NOVÁK I. 1989: [List of localities and their codes for mapping of the Czechoslovak entomofauna]. *Zpr. Čs. Společ. Entomol. ČSAV* **25**: 3-84 (in Czech).
- PETRBOK J. 1943: [Monographic study of the Bohemian molluscs of the genus *Tachea* and *Eulota*]. *Rozpr. II Tř. Čes. Akad.* **50**(13): 1-30 (in Czech).
- RAFIŃSKI J. 1981: Genetic polymorphism of an isolated urban population of *Cepaea nemoralis* (L.) at the eastern limit of its range. *Genet. Pol.* **22**: 329-339.
- RAMOS M. A. 1984: Polymorphism of *Cepaea nemoralis* (Gastropoda, Helicidae) in the Spanish occidental Pyrenees. *Malacologia* **25**: 325-341.
- RAMOS M. A. 1985: Shell polymorphism in a southern peripheral population of *Cepaea nemoralis* (L.) (Pulmonata: Helicidae) in Spain. *Biol. J. Linn. Soc.* **25**: 197-208.
- RATEL M. O., GÉNÉRMONT J. & LAMOTTE M. 1989: Relation entre polymorphisme et milieu chez les *Cepaea nemoralis* (Moll. Pulmonés) de la région Parisienne. *Bull. Soc. Zool. Fr.* **113**: 145-154.
- SCHILDER F. A. & SCHILDER M. 1953: Die Banderschnecken. Eine Studie zur Evolution der Tiere. Jena: VEB G. Fischer Verlag, pp: 1-92.
- SCHILDER F. A. & SCHILDER M. 1957: Die Banderschnecken. Eine Studie zur Evolution der Tiere. Schluss: Die Banderschnecken Europas. Jena: VEB G. Fischer, pp: 93-206.
- SLAVÍK A. 1868: [A monograph of terrestrial and aquatic molluscs of Bohemian]. *Arch. Přírodověd. Prozkoumání Čech.* **1**: 79-133 (in Czech).
- SLAVÍK B. 1971: [Cartographic grid for the prepared phytogeographic atlas of ČSR]. *Rozpr. Čs. Bot. Spol. ČSAV* **6**: 55-63 (in Czech).
- SOBOTKA M. 1945: [*Tachea nemoralis* from Skřivany near Nový Bydžov]. *Příroda* **37**: 254 (in Czech).
- WALL S., CARTER M. A. & CLARKE B. 1980: Temporal changes of gene frequencies in *Cepaea hortensis*. *Biol. J. Linn. Soc.* **14**: 303-317.
- WOLDA H. 1969: Stability of a steep cline in morph frequencies of the snail *Cepaea nemoralis* (L.). *J. Anim. Ecol.* **38**: 623 - 635.

APPENDICES 1 AND 2

The frequency of shell colour and banding morphs in local populations of *C. hortensis* and *C. nemoralis*. GN - geographic position of the locality indicated by the number of square in the reference grid used for faunistic mapping of the Czech Republic (see Material and Methods).

		Appendix 1: <i>Cepaea hortensis</i>																						
		FREQUENCY OF COLOUR AND SHELL BANDING MORPHS																						
		YELLOW										PINK												
GN	Locality	00000	12345	1(23)45	1(23)45	1(2)345	1(23)(45)	1(2)3(45)	1(234)5	1(23)(45)	1(2345)	Others	Total yellow	00000	12345	123(45)	1(23)45	1(2)3(45)	1(23)(45)	1(2345)	Others	Total red	Grand total	
5255	Horní Paseky		21										21										0	21
5352	Kravaře		27		1								28										0	28
5352	Kravaře	4	8										12	3	5								8	20
5353	Zahrádky		33	4									37	12	1								13	50
5355	Osečná	52	10						4			2	68		1	1							2	70
5357	Železný Brod	1	15										18	4							2		4	22
5357	Železný Brod		19										19	1									1	20
5359	Jilemnice		65										65										0	65
5452	Dřevčice	8	19										27										0	27
5453	Pavlovice		35	1	2	4						2	44	9									9	53
5453	Zakšín	50	42	6			3		1	1		5	108										0	108
5453	Dubá		131	25								3	162		6	1	1						8	170
5453	Berštejn	1	31	7	1					1	1		45	1							2	1	1	46
5453	Vrchovany		29		1								30										0	30
5453	Chlum		32	7		11		12		3	19	2	86										0	86
5453	Doksy		26									1	27										0	27
5455	Klášter Hradiště	6	16			1						2	25	3									3	28
5457	Rovensko pod Troskami	39	23		6	2				2		1	73	5									5	78
5463	Broumov	86	7									1	94										0	94
5555	Kosmonosy	6	2									2	10	13	1						1		15	25
5557	Sobotka		12	1	3	1	1	1	1	1	1	1	24										0	24
5558	Jičín	1	10	1	3		2			1	4	3	27										0	27
5558	Jičín	67	39	1	21					1	4	1	144	3									3	147
5558	Jičín	20	2				2						24	1									1	25
5558	Jičín	28	11		1	3					2	1	46	43									43	89
5559	Nová Paka	39	14		4	3	1	2	4	1		4	75										0	75
5559	Lázně Bělohrad	40	77	8	10	6	2	5		4	22	5	187										0	187
5559	Lázně Bělohrad	20	21	3	5		4	1			8		69										0	69
5559	Miletín	13	51	11	1		2					2	80										0	80
5560	Miletín	1	15	2	4					2	4	1	29										0	29
5560	Dvůr Králové	17	64		3	4						1	89										0	89
5560	Dvůr Králové	6	15										21										0	21
5561	Chvalkovice	3	37	2									42										0	42
5643	Hroznětín		31										31										0	31
5644	Pernštejn	7	15										22										0	22
5655	Dobruška	4	16	5	5	2	1	4		5	3	5	50	11									11	61
5657	Kopidno	11	2	3	4		1	1				9	7										0	38
5658	Nemyčevce	18	4										22										0	22
5658	Vysoké Veselí	26	11	4								1	42	15	5	2							23	65
5658	Chomutice		15	2	2		1	6	2	9	2	39											0	39
5658	Chomutice	3	13	2	5	1	1	1	1	7	1	34											0	34
5659	Vojice	9	29	7	34	1	14	1		3	7	4	109										0	109
5659	Ostroměň		91		49	2			1	4	2		149										0	149
5659	Ostroměň	20										1	21										0	21
5661	Jásenná		23	2		1		2			4	1	33										0	33
5740	Luby u Chebu	10	7										17	3									3	20
5740	Nový Kostel		13		6					1			20										0	20
5740	Kopanina		51	2		2		1					56										0	56
5742	Chodov		40	1									41										0	41
5742	Božičany		50			2							52										0	52
5742	Děpořovice		23										23										0	23
5743	Karlovy Vary	3	30										33										0	33
5743	Karlovy Vary	9	49			1				1		1	61	1	2								3	64
5743	Karlovy Vary		100										100	15									15	115
5743	Karlovy Vary	2	23										25		1								1	26
5743	Karlovy Vary	18	20										38	3	2								5	43
5745	Mašťov		10	1		1		1					13	16									16	29
5757	Městec Králové	21	8					2		2			33										0	33
5757	Městec Králové		10		12				2	3	3	2	32										0	32
5758	Chroustov	2	12	9		2	1	14				10	55										0	55
5758	Nový Bydžov	7	5	2								1	6										0	21
5758	Nový Bydžov	34	2			1		2				1	40	14	4								21	61
5759	Nechanice	22	8	1						1	2		34	13	1	1	1					2	25	59
5759	Nechanice	2	22										24		13								13	37
5760	Stěžery	112	5	2									119										0	119
5760	Hradec Králové	28	6	18		3	1	4				11	79										0	79
5760	Hradec Králové	46	23				1	2				2	74										0	74
5760	Hradec Králové	59	5										64										0	64
5761	Černilov	37			1	3		7			8	7	63										0	63
5761	Černilov	138	1										139										0	139
5848	Rakovník		32						1	1			34	5									5	39
5848	Lužná u Rakovníka	25	2										27										0	27
5849	Nové Strašecí	35	7										43										0	43
5849	Stochov		19		3					1			23										0	23
5851	Číčovice		39										39										0	39
5852	Praha		88										88										0	88
5853	Radonice		17										17	16									16	33
5854	Čelákovice	27											27										0	27
5858	Chlumeck nad Cidlinou	21	1									1	4										0	27

Appendix 2: *Cepaea nemoralis*

		FREQUENCY OF COLOUR AND SHELL BANDING MORPHS																														
		YELLOW										PINK																				
GN	Locality	00000	00300	00340	00345	003(45)	12345	123(45)	1(23)45	1(23)45	1(23)(45)	1(23)(45)	1(23)(45)	1(2345)	Others	Total yellow	00000	00300	00340	00345	003(45)	12345	123(45)	1(23)45	1(23)45	1(23)(45)	1(23)(45)	1(23)(45)	1(2345)	Others	Total red	Grand total
4951	Lobendava	12			1	11									25	7					5								15	40		
4952	Šluknov	45			5	1	13		2	1					70	2	25				2	2							37	107		
4952	Šluknov				5		11	1							17		4												6	23		
4955	Andělka	10													10	40	1				15	8	1	1	1	15	2		84	94		
4956	Ves					1									1	4	3				3		3	1	1	2			16	17		
5052	Mikulášovičky				14	1	20		1						36	1	33				33		2	1	1	2			73	109		
5052	Mikulášovice					1									1	1					20	4	1	2	2	2	1	1	33	34		
5052	Brtniky				9		9	5			4	1	1		29		15				9	5		7	1	1	1	1	38	68		
5052	Krásná Lípa						4								4	1					3		2		3	1			10	14		
5052	Krásná Lípa				12		19	2		1	1	8	1	5	49		5				13	3		1	3	1	8	1	33	82		
5052	Krásná Lípa				1		55	7	2			10	6	1	82		1				38	9	1	1	3	4			57	139		
5052	Krásná Lípa						58	2		5		2	3	2	72						34	4		3	2	2	8	1	54	126		
5052	Krásná Lípa						10			1		2	1		15		1				19	1		10	4			1	36	51		
5052	Krásná Lípa						37	8				2	4	2	53						31	15			4	7	2		59	112		
5053	Studánka				16		19	1	1			2	6	5	54						1			1	2			4	58			
5056	Vířňová				12		6			3					21	2	8				5		4	3	1	2			25	46		
5056	Víska						3			1					4	4					4	1		4	3				16	20		
5056	Kunratice				2		1		6	1	2	6			18	37	9		4	1	23	3	1	13	21	5		117	135			
5056	Dolní Řanovice				6	3			18	5		9	1		42	23	5				6	5		9				48	90			
5056	Krásný Les				1	8			9			3	1		22	8	12				6	3	1	7	1	1	1	39	61			
5056	Arnoltice				1		1		1	3					6	21	10		1		4	5		5	5			46	52			
5056	Frydlant v Čechách						20	7			5	1			33	7					10	4	1	2	4	3		31	64			
5056	Raspenava				1		1	1			2				6	2	3		1	1	3	7		27	6			50	56			
5057	Jindřichovice				37		4	3	9	4		1	2	2	64	52	57				6	4	8	6		8	3	144	208			
5057	Nové Město				49		7	7	2	2					67	5	31		9	5		1	1	3		1		56	123			
5057	Nové Město				30		8	4	17	5	1				86	13	8		1	4	5	2		2	1			36	102			
5152	Chřibská				1		12	3		4	2	1			23	1					3	1		3	4			13	36			
5152	Chřibská						10	10		4	13	1	3		41	26					5	6	3	14	4			58	99			
5152	Jetřichovice						1				5	7	3		16						1	1		4	2	2		10	26			
5153	Dolní Podluží						34	4	3	9	5	5	2	2	84						15	7	1	9	4	3	21	1	61	125		
5153	Dolní Podluží						34	1			4	1			40						7		1	1	2	2			13	53		
5153	Jičetín pod Jedlovou				2		18			1					21	23					8	2		1	1	1	1	36	57			
5153	Rybníště				3		20	2		1	1	2	2		31	22	11				7	1	1	3	1	1	1	47	78			
5154	Meřence						12	4	2	2	2	1	5		28	34					2			1	1	1			38	66		
5155	Chrastava				1		2	1	18	1	3	4			21		1				1	1	1	1	2	1		7	38			
5157	Bílý Potok				13	11		3	2	12	2	6	7	1	57	17	4				1	1	1	1	1			25	82			
5252	Volfartice														0						58	2		1					61	61		
5253	Nový Bor						9			1					10	14					5			1	1	1			21	31		
5253	Nový Bor						26	1	1	4	1		1		34	16					9	1	1		2			29	63			
5253	Nový Bor						7	1	1		2				11	43					3				1			47	58			
5253	Chotovice				1		18	2				2			23	9					2	1			1			13	36			
5253	Sloup						14								14						1								1	15		
5253	Manušice						9		1						12														0	12		
5254	Jablouň						16	6		2	8	14	4		50	8					7	1	1	3	1	12	2		35	85		
5254	Jablouň						5				3				8	5					4			3	3				15	23		
5254	Stráž pod Ralskem						29	14			2				45	45					19	8	2	2	1	1	1	78	123			
5254	Stráž pod Ralskem				1		12	7			7				27	65					13	7	6	16	1			108	135			
5255	Hammr						65	1	1						67						24	1							25	92		
5255	Břevniště						1				1				2						16	4	2	5	4	2			33	35		
5255	Osečná						7	1	1						9						3								3	12		
5255	Křížany						9	7			10			1	27	2					6	16	2	85	3	1		115	142			
5256	Liberec				6	1			6	3	1	2			19	44	4				11	1					1	61	81			
5256	Liberec				2				2	3		1			8	10					1	3	5		2			21	29			
5256	Liberec						1								1	12					4	2	1	2	1			22	23			
5256	Vratislavice				2			9	2			1			14	2	1				6	4		5	1			19	33			
5257	Janov nad Nisou						2								4	4	20		1	2	3	1		7	3	1	42	46				
5257	Josefův Důl						6		1	1	1	1			9						3		1	3				7	16			
5257	Lučany						5				2				7	1	2				3	2						8	15			
5257	Lučany						2								2							1	1	7			3	14	16			
5257	Tanvald						1								1						8	2		7	15	1	26	1	62	63		
5257	Vrkoslavice						3								4	16					10	4	1	5	1	1		38	42			
5353	Česká Lípa				9	6				15	2	2	6	1	10	1	5	57			15	4	1		5	2	5	2	64	121		
5353	Česká Lípa						24	1				2	5	2	1	35					34	10	3	9	7	1	11	3	78	113		
5353	Česká Lípa						6	1				1	2		10	14					8	1		3	1			27	37			
5354	Mimoň						91	10		2	8	1			112	7					24	4	1	4	1	1	1	42	154			
5355	Hodkovice						43	45		13					102	13					1								14	118		
5355	Hodkovice						11	4				6			21	16					1								17	38		
5356	Rychnov nad Nisou						19	3		3	1				26	15					19	5		5	1			45	71			
5356	Český Dub														0						15	34	1	43	7	1		101	101			
5356	Sedlšířka														3		25					1		2	6			34	37			
5357	Držkov						8	3		2	5	1			19						1	2		1	1							

5450	Litoměřice	10	12	8	3	1			2	1	1	1	39	2	51		7	2	4			4	1	3	74	113				
5450	Litoměřice	11			1				2		5	2	21		29		1		1	3		1	4	4	5	2	50	71		
5450	Litoměřice	4	9	2	3	10	1				1	2	32	35	19		5	6	7	4			4	5	3	3	91	123		
5450	Litoměřice	1				2	1			4			8	1	18		1	1	1	1		3					26	34		
5450	Litoměřice	8	1	3	2	3	4		1	2	1	1	26	11	12		1	3			1						28	54		
5450	Litoměřice	42		5	5	3	3			8	13	1	81	13	64		2	5	2				3	3	1		93	174		
5450	Litoměřice	7				4						1	12		5												5	17		
5450	Litoměřice	32	4	1	9	8		1	14		3	2	1	75	30	3							1	1			35	110		
5450	Litoměřice	18		1	2	1	1			1			1	25	3	8								2			13	38		
5450	Litoměřice	1	22			7	1					2	5	1	39					2	1		1	4	1		24	63		
5450	Litoměřice	2	33	5	4	6	3			6	2	1	62	20	19			1	6	1		1		1	2	51	113			
5450	Litoměřice	2	2			1				1			6		1								1		1		5	11		
5450	Litoměřice	4	44	7	16	6	6		1	10	4	2	1	101	24	39		8	4	7	3		1	2	4	1	3	96	197	
5450	Litoměřice	76		5	2	1	1		2	3		5	95	29	41					3	1		1				75	170		
5450	Litoměřice	1	17	1	1	9	5			7	2	1	2	48	28	28		1	4	4	4	1	13	7			90	136		
5450	Litoměřice	16		3	2	2		1	1	1			26	24	26		3	2	8	3		1	15	5	2	94	120			
5450	Litoměřice	12	1	15	5	3	1			2	1		1	41	47	36		15	12	4		1	8	3	1	2	129	170		
5450	Litoměřice	108		12	1	83	4		1	6	2	4	201	12	8					1	1						22	223		
5450	Litoměřice	1	142	7	5	17	10			3	10	3	6	204		21		2	2	1	1		2	2	1		32	236		
5450	Litoměřice	21	59	37	11	4	22	20		2	2	12	190	4	13	7	2	3	5	3					1	2	40	230		
5450	Litoměřice	52		2	3	1	6		2		2	1	89		17	1		2	1						1		22	91		
5450	Litoměřice	11		2	6	3	2		7		2		33	1	10	1	1	1	1	2		2	3	3	1		26	59		
5450	Mlékojedy	18	2			5	2		2	4		33	1	26		1	2	6				7	5	3			51	84		
5450	Želetice	1				3				2	1		7		22		1		1	5		3	4				36	43		
5451	Liběšice	1	12		2	1	1						17		28		2	1					2				31	48		
5451	Počaply	22			2		1						25	2	31		1	1									35	80		
5451	Počaply	36		5	1	3			2	1			48	5	22							1	1				29	77		
5451	Terazín	1	16		1								18	18	110		10	6			1		1				146	164		
5453	Staré Splavy					26				3	1		30							13	1	3	1	1	1	2	7	29	59	
5460	Hostinné					3	4		1	18	1		27														0	27		
5464	Broumov	5	7		1	13	3	2	1	1			33	30	28		2		10	4	4	1	2	2	3		86	119		
5550	Bohušovice	21		2		4			1				28	14	16		1	2	2				2				37	65		
5550	Keblice	5				2		1	1	6	1	1	17		2												2	19		
5557	Sobotka			24	11	9		5	18	5	32	7	111														0	111		
5559	Nová Paka												0		174				3	2			2	1			182	182		
5559	Nová Paka	3			12	14		1	15			2	47					7	5			11	1				24	71		
5560	Miletín	2											2	16	4	1												23	25	
5658	Millčevce					2		1					3		4	1	31		25	1						30	82	95		
5658	Slatina			9	10				8	1			28							3			3				6	34		
5658	Hradištko			10	8							1	19				4		7			1				7	19	38		
5658	Vysoká Veselí	35				22	8		7	1	1	2	76		51			14	17		3	28	1			114	190			
5658	Chotutice	10			18	2		1	10				41	11	1			9	2		1	4	1			29	70			
5658	Žunice	45			33	6		4	8			1	97		32			3	1	1		1	2			40	137			
5659	Ostroměř	5				1							6	18													18	24		
5659	Ostroměř					1	1			6		1	9	12												1	13	22		
5659	Hořice	3				1							4	50	17					2		2	7				78	82		
5659	Hořice												0						1	4		1	3	2			11	11		
5659	Lískovice	2			7	5			2				16		1					1							2	18		
5662	Česká Skalce					15	1	1		4	2	1	24	61					4	2			2	1	3		73	87		
5758	Kněžice	7		4	4								1	16	1	8		4	9								22	38		
5758	Smidary	7		2		30	6		2	12			9	68					37	21		3	32	1	5	99	167			
5758	Janovice	47				19	5		1			3	75		7				3	1		1					12	87		
5758	Hlušice	5				3	1		1	2			1	13		3											3	16		
5758	Hlušice	56	1			15	1	2	1	3	1	1	82		21				2				1	1			25	107		
5758	Starý Bydžov	62		2		18	10						93														7	100		
5758	Starý Bydžov	33				14	4					1	52		39				12	11		1	6		1	70	122			
5758	Nový Bydžov	22				5	4		1				32	1	3								1	1	1		7	39		
5758	Nový Bydžov	16											16		12												12	28		
5758	Nový Bydžov	17				2			1			1	21		5								1				6	27		
5758	Nový Bydžov	41				1	1					1	44		6					1							7	51		
5758	Nový Bydžov	104				23	10		1	9	2	3	2	154		7				1			1				9	163		
5758	Nový Bydžov	68				11	5			3	1	3	1	92		10				1			1				12	104		
5758	Nový Bydžov	49				1							50		17												17	87		
5758	Nový Bydžov	5											5		4					1	1						6	11		
5758	Nový Bydžov	15				5	3			1			24		8					4							12	36		
5758	Nový Bydžov	17		1		1	1					1	21														0	21		
5758	Nový Bydžov	4	95			4							103		2												2	105		
5758	Nový Bydžov	5	29		2		8	6					50	1	3					1							5	55		
5758	Nový Bydžov	23				7	2			2			34		6					1							7	41		
5758	Nový Bydžov	16				5						1	22		5					2							7	29		
5758	Nový Bydžov	72				13	2			3		1	91		39				1	8			2				48	139		
5758	Nový Bydžov	44				8	5			3		1	61		29					3			2				34	95		
5758	Nový Bydžov	43				44	2					1	90		31				20	2		1					54	144		
5758	Nový Bydžov	59		3		25	12		2	7	4	1	18	131		63			22	21		1	10	3	2	3	125	256		
5758	Nový Bydžov	17				9	5			5			36		25				10	11										