

CEPAEA NEMORALIS (L.) IN GÖTEBORG, S.W. SWEDEN: VARIATION IN A RECENT URBAN INVADER

ROBERT A. D. CAMERON^{1,2}, RHONA J. COX³, TED VON PROSCHWITZ⁴, MICHAL HORSÁK⁵

¹ Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
(e-mail: r.cameron@sheffield.ac.uk)

² Department of Zoology, the Natural History Museum, London SW7 5BD, UK

³ AstraZeneca, Pepparedsleden, 431 83 Mölndal, Sweden

⁴ Section of Invertebrate Zoology, Göteborg Natural History Museum, PO Box 7283, SE-40235 Göteborg, Sweden

⁵ Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic

ABSTRACT: Although present since the mid 19th century, the introduced snail species *Cepaea nemoralis* has spread extensively in Göteborg, mainly in the last two decades. Early samples show the predominance of yellow-shelled morphs, but in modern populations pink shells predominate. There is great variation in morph frequencies among modern populations with high values of F_{ST} and with no relationships to habitat. The patterns shown resemble those seen in Sheffield (UK), a city also colonised over a similar time period, but differ from those seen in regions where the species has been established for much longer. The combination of early and recent records suggests not only that founder effects play a large part in determining morph frequencies, but that present populations derive from multiple colonisations from different sources.

KEY WORDS: *Cepaea nemoralis*, polymorphism, invasion, Göteborg

INTRODUCTION

The numerous studies on the shell colour and banding polymorphism of the European land snail *Cepaea nemoralis* (L.) have revealed a great variety of patterns of variation (JONES et al. 1977, COOK 1998). While there is no doubt that natural selection influences these patterns in many cases even if the agencies involved are unknown (OŽGO 2008, SILVERTOWN et al. 2011), there is also evidence that founder effects and the balance between genetic drift and gene flow also affect such patterns (COOK 1998). This is especially true where populations have been small and isolated in the past (CAMERON & DILLON 1984), or where *C. nemoralis* has recently colonised previously unoccupied areas, usually assisted by accidental transport by humans (CAMERON et al. 2009). Even in such cases, however, evidence of rapid selection in relation to the shade or darkness of the habitat or to a measurable change in macroclimate has sometimes been found (OŽGO 2005, 2011, OŽGO

& KINNISON 2008, OŽGO & SCHILTHUIZEN 2011, SILVERTOWN et al. 2011, CAMERON et al. 2013). The known genetic basis for most of the polymorphism makes the species a good model organism for studying the mechanics of evolutionary processes over a range of time-spans (OŽGO 2008, 2014).

While *C. nemoralis* has become less frequent and widely-distributed in parts of its range (COWIE & JONES 1987), it has also colonised previously unoccupied areas, both within its assumed natural range and in places where it has been introduced beyond it, especially towards the eastern half of Europe (OŽGO 2005, PELTANOVÁ et al. 2012). The species is well-adapted to human-made habitats such as hedges, waste ground and gardens, and it has spread rapidly in many cities. CAMERON et al. (2009) examined variation in two cities, Sheffield in central England and Wrocław in S.W. Poland. Although Sheffield is within the natural range of the species, its occupa-

tion of the city has been very recent, following great reductions in industrial pollution. Wrocław was colonised earlier; it is questionable whether it lies within the natural range. There were marked differences in the pattern of variation between the two cities; while neither showed any effect of habitat on morph frequencies, variation among populations was much less in Wrocław and populations were more polymorphic. This was attributed to a longer time present in the city, and greater continuity and therefore gene flow among populations.

The evidence from Holocene deposits indicates that *C. nemoralis* is an introduced species in Sweden (WALDÉN 1986). While fossil records from the Middle Ages suggest that it has been established for several centuries in the extreme south (Skåne) of the country, it has spread recently over much of Sweden south of ca. 59°N, and has very recently been found even further north (T. VON PROSCHWITZ, unpublished data). The oldest record of *C. nemoralis* in Göteborg (57.7°N) is from the beginning of the 1850s (MALM 1851). At that time the species must have been a very rare element, and only one further occurrence (from a cemetery about 2 km from the original site) is known from the 19th century. In 1921–1922 the land snail fauna in 148 sites in the city and its immedi-

ate surroundings was investigated and showed only three localities for *C. nemoralis* (LOHMANDER 1923). The series consisted both of natural and strongly man-influenced / man-made habitats. The same sites were re-investigated in the 1970s, when the number of localities holding *C. nemoralis* had increased only moderately to seven (WALDÉN 1992). The polymorphism in a population detected in 1967 in Askim, ca. 12 km south of the centre of the city, was described by MEEUSE (1968). In an investigation of 37 man-made and strongly man-influenced sites in 1978–1986, all of which must be considered as suitable for *C. nemoralis*, it was found in ten (VON PROSCHWITZ 1988). Today the species occurs in many of these sites. There is thus good reason to believe that the present common occurrence of *C. nemoralis* in Göteborg is a result of increased spread during a rather short period, mainly in the last two decades.

The city has a metropolitan area and human population very similar to those of Sheffield and Wrocław. In this paper, we analyse the variation of *C. nemoralis* populations in Göteborg. Apart from comparisons with the other two cities using recent records, the earlier records enable us, with reservations, to track changes in frequencies with time, and relate these to the process of spread.

AREA STUDIED

Recent and historic records of *C. nemoralis* in the vicinity of Göteborg include a number from rural locations some distance from the city, and from small islands to the west. Most, however, come from urban environments within the city or its neighbouring towns. To make comparisons with the entirely urban populations sampled in Sheffield and Wrocław, we have confined our analyses to sites lying within the rectangle defined as between 11.8 and 12.2°E and

57.6 and 57.8°N, an area of ca. 540 km² (Fig. 1). This area excludes offshore islands and the rural hinterland of the city. The topography is one of small hills and valleys on a granite platform. The city receives ca. 780 mm of precipitation per year, with significant rainfall in all months. January mean temperature is ca. -1.5°C and for July ca. 16°C. Comparable data for Sheffield are 800 mm, 3.8 and 16.2°C, and for Wrocław 570 mm, -0.5 and 19.9°C.

MATERIAL AND METHODS

The samples of *C. nemoralis* have three sources. The first is the lots of specimens held in the Göteborg Natural History Museum. These were collected by a number of people, but were all scored for shell variation by TED VON PROSCHWITZ (see below). The earliest sample comes from a site described as Dahlin's garden or meadow, made in the 1850s. This site was sampled on a number of occasions in the 19th century, but it changed during that century as a result of development, and now holds apartment blocks. There are a few samples from the first 70 years of the 20th century, but most consist of single or only a few shells. From 1975, and especially since 1990, there are more and larger samples available.

The second source is a single sample reported by MEEUSE (1968) at Askim, south-west of the city centre (Fig. 1), scored by Meeuse himself and accompanied by extensive ecological notes. He distinguished between "red", "reddish yellow" and "yellow" shells. All the "reddish yellow" shells were banded, and we have assumed that all these and those in the "red" category were pink in the conventional scoring system outlined in JONES et al. (1977); banding usually dilutes the strength of the shell colour in pink shells.

The third source is samples made by RHONA COX and ROBERT and ALEXANDER CAMERON in 2012 and 2013. These samples were scored in the field, and live snails were returned to the habitat in which they

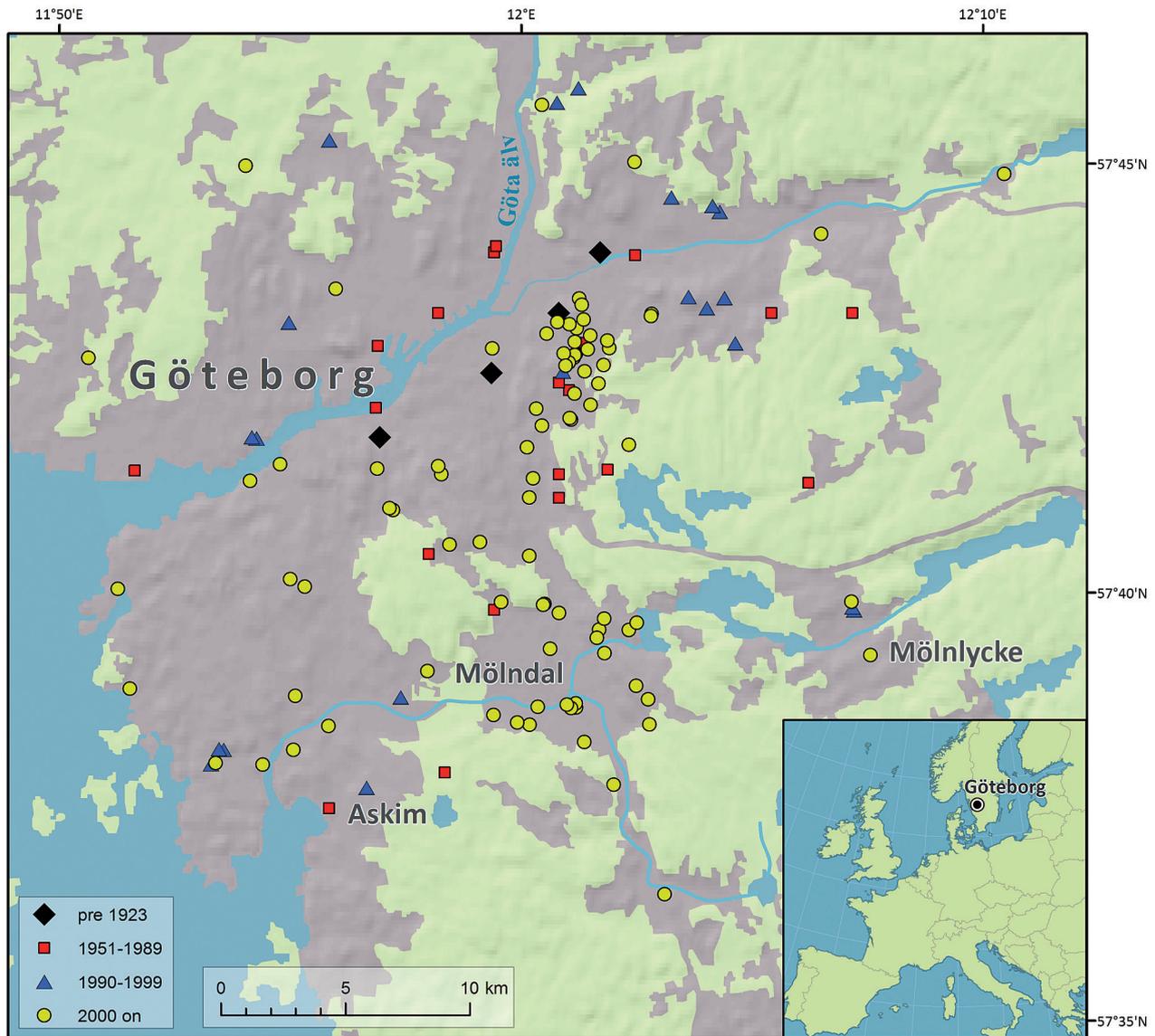


Fig. 1. The area sampled, and site locations. Large black diamonds – pre-1923, red squares – 1951–1989, blue triangles – 1990–1999, yellow circles – 2000 onwards. Built up areas shown in grey

were found. The habitats in which these samples were made were classified as shaded (usually in urban woodland) or open, where the site was not overshadowed by trees. This classification was necessarily imprecise, though made by the same observers; urban habitats are frequently very heterogeneous even within very small areas. The presence or absence of the closely-related *Cepaea hortensis* (Müller) was noted for each site. Only adult snails or large juveniles in which the dark colour of the lip was emerging were scored to avoid any confusion with that species. A few dissections of white-lipped adults were carried out. All white-lipped snails were *C. hortensis*; these were much smaller than *C. nemoralis*. Samples from the first and second sources were located by reference to streets or addresses; those from the third by GPS on site. Site co-ordinates have been standardised to decimal degrees.

Scoring of colour and banding morphs basically followed the system outlined by JONES et al. (1977). Scoring of banding variation was done in more detail for the samples held in the Natural History Museum than for those scored in the field, with precise notes on the fusion of bands and of the absence of individual bands. These details and the whole data set are available as a digital archive from the Göteborg Natural History Museum at www.gnm.se/cepaea. For the analysis, three colours: yellow, pink and brown, and four banding categories: unbanded, mid-banded (00300), trifasciate (00345), and many-banded (12345) were recognised (JONES et al. 1977), with minor variants being allocated to the most appropriate class. Thus 00045 shells were allocated to the trifasciate class, and 10345 to the many-banded class. The genetics of the classes recognised is well-known; that of fusions of bands is not, and it is difficult to

standardise recording among observers. Only samples containing 10 or more scoreable shells were used in formal analyses.

The distinction between pink and brown shells is not always easy. Most brown shells sampled were dark and unbanded, but in a few cases banded shells may have been misallocated. A more serious problem concerns the colour of old specimens, as colours fade even in specimens kept in the dark. As shown later, there is a highly significant decline in the proportion of yellow shells over time, with early (pre-1990) samples containing mostly shells scored as yellow. Great care was taken in scoring these early samples. For the main analysis, however, we have considered only samples made since 1990; in any case the primary aim was to examine current patterns of variation.

In all analyses, we have used morph frequencies, not estimated allele frequencies. For midbanded the frequencies are those within the banded shells; for trifasciate they are those within shells with more than one band, reflecting the dominance hierarchy at these loci (JONES et al. 1977). Where regression or least squares correlation has been used all these frequencies have been arcsine transformed. Besides

tests of association of morphs with each other and with position and habitat, we have examined the linkage disequilibrium between shell colour and banding, taking simply the proportion of unbanded shells within each colour class and other associations among colour and banding classes.

Following CAMERON et al. (2009), spatial pattern has been examined using Moran's I for the frequencies of yellow, brown, unbanded, mid-banded in banded and trifasciate in many-banded. Overall genetic similarity has been analysed by Principal Components Analysis (PCA) using the same frequencies and Moran's I has been calculated also for the site scores at the first two PCA axes. Variation within and among populations has been estimated by the proportion of samples visibly monomorphic at each locus, by the proportions of samples with different numbers of morphs present, and by estimating F_{ST} based on morph frequencies (CAMERON et al. 2009). We estimated means and standard deviations of these F_{ST} values using a bootstrapping procedure with 10,000 permutations. The software used for the analyses comprised: SAM (RANGEL et al. 2006) for Moran's I and R (R CORE TEAM 2012) for all the others.

RESULTS

SITE DISTRIBUTION AND VARIATION OVER TIME

Appendix Table 1a gives details of all samples held in the Göteborg Natural History Museum and that of MEEUSE (1968) in date order. Appendix Table 1b gives details of all samples scored in the field in 2012/13. The more detailed scores and locality details for samples in Appendix Table 1a are available as a digital archive from the Göteborg Natural History Museum (see above). Figure 1 shows the distribution of sampling sites within the study area. There are very few sites that have been sampled on more than one occasion, and with the exception of the first site at which *C. nemoralis* was found (Dahlin's garden), such a repeat sample was made within only a few years of the original and we have combined the samples to give an aggregate score. We cannot follow any changes with time on a site-by-site basis. Any apparent change in mean or median frequencies over time could thus result simply from the sampling of different sites; even within 21st century samples, the range of frequencies recorded is great (see below). The number of samples in some ranges of dates is also small. Nevertheless, inspection of the data demonstrates a substantial decline in the frequency of yellow shells over time, perhaps complicated by the difficulty of accurately scoring shells stored for several decades.

In the period from 1850 to 1922 there are records from only five sites, one of which is not precisely located. Five samples come from the first recorded locality (Dahlin's garden), and were made over a period of around 40 years. The earliest, containing only two shells, was made in the 1850s. All but one of the shells collected are yellow, and all fall into the trifasciate or many-banded categories (Table 1). There are significant variations in the proportions of these two forms between sampling occasions, but no consistent trend with time. No unbanded or midbanded shells were found. In the remaining samples from this period no pink shells were recorded, but a few unbanded and mid-banded shells were present.

No samples are held in the Göteborg Natural History Museum for the period 1923–1950. The frequencies of yellow shells in later samples are shown in Table 2. The small samples made between 1951 and 1989 are predominantly yellow. In the first part of this period, all samples are small, but from 1967 to 1985 there are ten samples with 10 or more shells. The frequency of yellow shells varies greatly among them. While the median is 62.3%, it is noticeable that these samples fall into two categories: those with less than 25% yellow shells (4) and those with more than 60% (6) (Appendix). There is no geographical pattern; samples with very different frequencies lie close together. Collectively, samples from this period contain some shells in all colour and banding combi-

Table 1. Variation in *C. nemoralis* made before 1923. In this and later tables: P – pink, Y – yellow, 0 – unbanded, 3 – mid-banded, tri – 00345 and variants, 5 – many banded with at least one of the top two bands (1 and 2) present

Location	Date	Shells	P0	P3	Ptri	P5	Y0	Y3	Ytri	Y5
Dahlin's garden 1	1850s	2							2	
Dahlin's garden 2	1873	20			1				19	
Dahlin's garden 3	1886	22							8	14
Dahlin's garden 4	Pre1900	25							4	21
Dahlin's garden 5	Pre 1900	28							14	14
Dahlin's garden total		97			1				47	49
Others (4 sites)	1886–1922	25					1	2	10	12

Table 2. The number of samples and shells, the percentage of yellow shells among them arranged by date and size (small – less than 10 shells, large – 10 or more). The percentage of yellow shells in total is given for small samples, and the range and median values for sets of large samples. The last row represents samples scored in the fields (C – samples made by RHONA COX and ROBERT & ALEXANDER CAMERON). The remainder, with the exception of the sample of MEEUSE (1968) were scored from lots held in the Göteborg Natural History Museum

Period and sample type	N samples	N shells	% Y	min	max	median
1951–1985 small	11	48	91.7			
1967–1985 large	10			18.2	100	62.3
1990–1999 small	17	58	37.9			
1990–1999 large	5			39.0	57.1	48.9
2000–2013 small	9	32	34.4			
2000–2013 large	11			6.3	100	38.1
2012–2013 C	68			0	91.7	36.1

nations except that brown banded shells are missing (Appendix).

Between 1990 and 1999 there are only five samples with 10 or more shells. The median frequency of yellow shells is just below 50%, and there is relatively little variation among them. Just less than 40% of shells in the 17 smaller samples are yellow. Among 21st century records medians are also below 40%, but the range of variation among samples is large. While this decline in the frequency of yellow shells with time is of interest, investigation of relationships with position or habitat, and estimates of the amount of variation among samples, needs to exclude systemic changes over time. For analysis of such patterns we have therefore confined formal analysis to samples of 10 or more shells made since 1990. There are no significant differences in median values of yellow among large samples from different periods after this date.

PATTERNS OF VARIATION IN MODERN SAMPLES

In total, 84 samples of more than 10 shells made since 1990 were available for the analysis (Table 3). No morph was present in all samples, and the range of recorded frequencies was great in all. Among the samples collected in 2012–2013 and scored in the field, there are no significant differences in any morph frequencies between shaded and open habitats overall (Table 4), and some of the small differ-

ences observed run counter to expectation; yellow has a higher median frequency in shaded than in open sites. In the classic Cain and Sheppard dia-

Table 3. The range, mean and median frequencies (%) of colour and banding morphs among the 84 samples of 10 or more shells made since 1990

Morph	min	max	mean	median
Yellow	0	100	38.0	38.1
Pink	0	100	58.8	59.1
Brown	0	70	3.2	0
Unbanded	0	74	14.6	5.6
Mid in banded	0	90	21.6	13.8
00345 in banded	0	100	47.1	46.4
5 banded in total	0	95	36.2	32.0

Table 4. Morph frequencies in samples from shaded and open habitats scored in the field. Upper rows – median frequencies of yellow (Y), pink (P), brown (B), unbanded (U), mid-banded (mid), trifasciate (tri) and many-banded (many). No difference between habitats is significant. Lower rows – number of nearest neighbour pairs in which the given morph is more frequent in each habitat

Habitat	n	Y	P	B	U	mid	tri	many
Shaded	21	39.0	51.8	0	9.3	18.8	50.0	32.4
Open	47	30.0	63.2	0	6.6	11.3	46.4	33.9
Pairs								
Shaded+	15	8	5	6	9	10	14	
Absent both	0	0	9	0	3	0	0	
Open+	6	13	7	15	9	11	7	

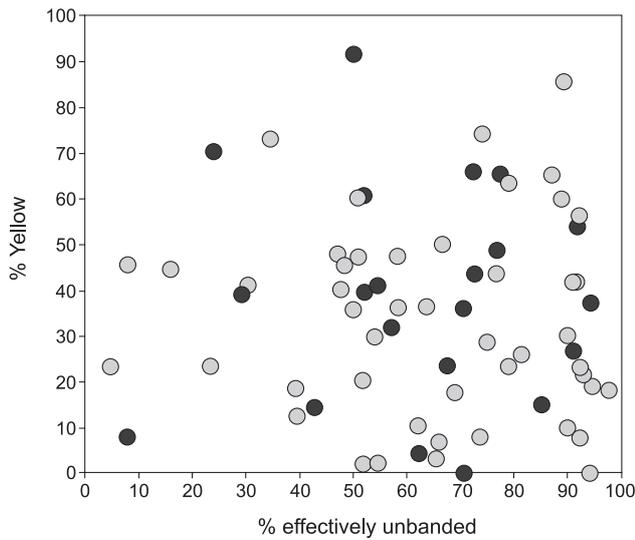


Fig. 2. The Cain and Sheppard diagram, the scatter of yellow and effectively unbanded frequencies among samples scored in the field, separated by habitat; solid black circles – shaded habitats, grey circles – open habitats. Effectively unbanded includes all shells in which the two uppermost bands are missing

gram (COOK 2008), where “effectively unbanded” represents the proportion of unbanded, midbanded and trifasciate shells in the total, samples lie mainly in the bottom right sector, and there is no clear pattern of difference between habitats (Fig. 2). When each shaded site is compared with its nearest open neighbour in a paired sample comparison, the same result is obtained (Table 4); indeed, the excess of pairs in which yellow is more frequent in the shaded habitat borders on formal significance ($\chi^2 = 3.85$). The lack of the expected trend is not a product of geographical differences in the distribution of habitats. We note that there is also no correlation in morph frequencies between members of each pair, even though the median distance separating each is only 0.6 km. Similarly, the recorded presence or absence of *C. hortensis* has no significant effect on median morph frequencies (data not shown). Within the whole data set, there are also no significant correlations for any morph with latitude or longitude; values of R, the correlation coefficients (calculated

Table 5. Within sample associations between colour and banding morphs for all samples in which there is variation in both. Y+, P+ – the number of samples in which the banding morph indicated is in excess in each colour. * – $P < 0.05$. % columns show the proportions of each banding morph in the total of shells scored. There are very few brown banded shells

	Y+	P+	χ^2	% in Y	% in P	% in B
Unbanded	15	32	4.78*	6.8	12.3	89.2
Mid-banded	27	40	2.52	23.3	21.5	
Trifasciate	30	36	0.55	42.3	45.3	

on arcsine transformed values) are generally less than 0.1.

With only one exception, there are no significant among-sample associations between morph frequencies at different loci. There is a weak association between the frequencies of brown and of unbanded shells; both morphs are absent from many samples, but where unbanded is present there is no difference in its median value between those samples that do or do not contain brown shells. Nearly all brown shells are unbanded (see below).

Associations between morphs at different loci within samples are similarly weak, with the excep-

Table 6. Values of Moran’s I for morphs and the first two PCA axes in each of four distance classes. Significant values of I are given in bold font; no adjustment for number of tests has been made

Distance class	Count	Moran's I	P	I (max)	I/I(max)
Yellow					
0–1.5 km	870	-0.006	0.904	0.432	-0.013
1.5–5.0 km	2020	0.016	0.523	0.401	0.040
5.0–8.5 km	2524	-0.019	0.350	0.297	-0.064
8.5–21.8 km	1558	-0.041	0.106	0.322	-0.127
Brown					
0–1.5 km	870	0.161	<0.001	0.818	0.197
1.5–5.0 km	2020	-0.058	0.018	0.340	-0.171
5.0–8.5 km	2524	-0.038	0.071	0.387	-0.097
8.5–21.8 km	1558	-0.008	0.661	0.329	-0.023
Unbanded					
0–1.5 km	870	0.086	0.027	0.573	0.151
1.5–5.0 km	2020	0.096	0.002	0.449	0.214
5.0–8.5 km	2524	-0.101	0.004	0.371	-0.271
8.5–21.8 km	1558	-0.064	0.032	0.624	-0.102
Midbanded in banded					
0–1.5 km	870	0.166	<0.001	0.757	0.219
1.5–5.0 km	2020	0.138	<0.001	0.449	0.307
5.0–8.5 km	2524	-0.201	<0.001	0.544	-0.369
8.5–21.8 km	1558	<0.001	0.998	0.336	<0.001
00345 in banded					
0–1.5 km	870	0.004	0.922	0.388	0.011
1.5–5.0 km	2020	-0.007	0.790	0.280	-0.027
5.0–8.5 km	2524	-0.026	0.225	0.241	-0.108
8.5–21.8 km	1558	-0.004	0.848	0.284	-0.016
PCA 1					
0–1.5 km	870	0.008	0.839	0.406	0.020
1.5–5.0 km	2020	-0.013	0.615	0.310	-0.042
5.0–8.5 km	2524	-0.022	0.303	0.257	-0.086
8.5–21.8 km	1558	-0.006	0.790	0.307	-0.019
PCA 2					
0–1.5 km	870	0.121	0.007	0.726	0.167
1.5–5.0 km	2020	0.132	<0.001	0.469	0.281
5.0–8.5 km	2524	-0.145	<0.001	0.518	-0.280
8.5–21.8 km	1558	-0.057	0.042	0.465	-0.123



tion of that between brown and unbanded (Table 5). Of 22 samples containing brown shells, 18 have only brown unbanded shells, and in every case unbanded has a higher frequency in brown than in either yellow or pink shells. There is a barely significant trend for unbanded to be in excess in pink rather than yellow shells (the loci are linked), but there are no significant associations between colour and mid-banded or trifasciate. A simple summation of all shells shows the same pattern.

Positive spatial autocorrelation in morph frequencies as estimated by Moran's I is present over short distances in the proportions of unbanded, mid-banded and brown shells, but not in those of yellow or trifasciate shells (Table 6). Figure 3 shows a distinct cluster of sites in which brown shells occur, although these are not the only sites to hold the morph. Despite the formal significance of these autocorrelations, the

associations are weak when contrasted with the maximum possible values of the index. In the PCA analysis (Fig. 4), the first axis is strongly correlated with the frequency of trifasciate and shows no spatial relationships. The second axis shows varying correlations with the other morphs, and also shows significant positive values of Moran's I at short distances. Site scores on this axis show a significant negative association with latitude ($R = 0.405$, $df 82$, $P < 0.001$), albeit with a wide scatter. No single morph showed a significant association with latitude (see above).

Values of F_{ST} estimated from morph frequencies are given in Table 7, together with the equivalent values for Sheffield and Wrocław. Table 8 shows the extent of visible monomorphy at those loci comparable across all three cities and Figure 5 shows the frequency distribution of samples with varying numbers of the six morphs that can be compared across

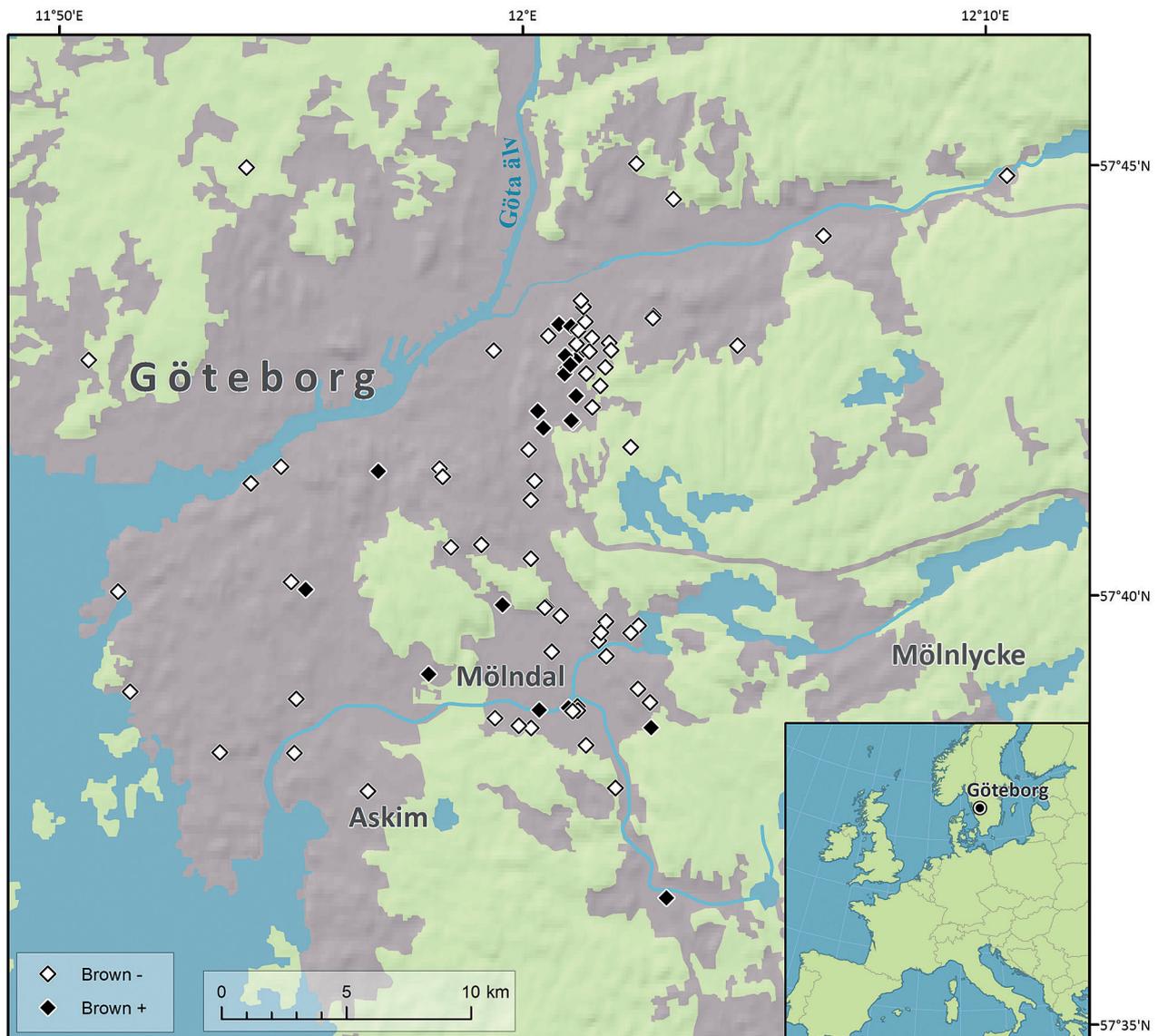


Fig. 3. The distribution of samples with brown shells (solid diamonds) and of those without brown shells (open diamonds)

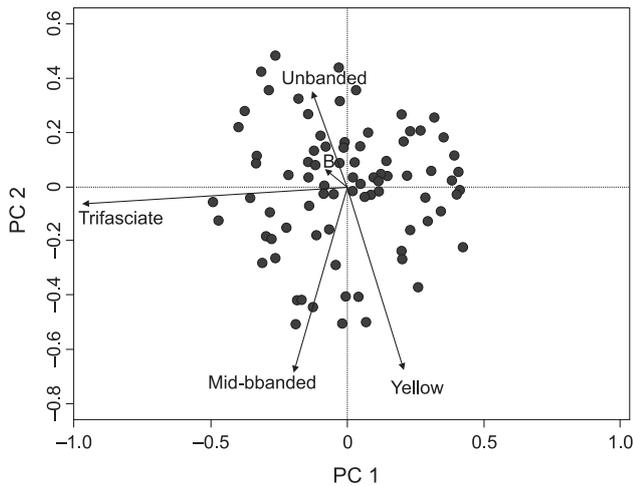


Fig. 4. The scatter of samples on the first two principal components of the PCA. The magnitude and direction of the relationship of each morph with the components is shown. B – brown

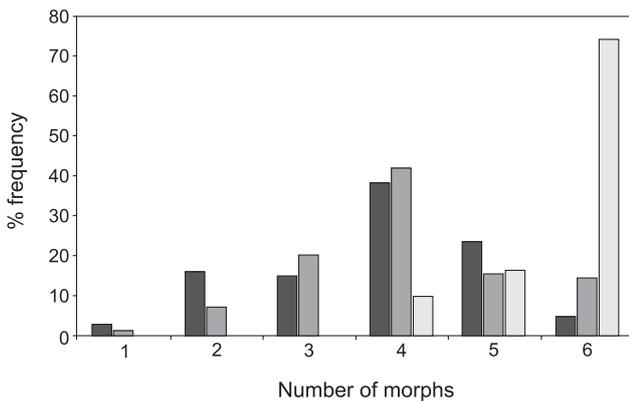


Fig. 5. Frequency distribution of samples with given numbers of morphs (maximum 6) in Sheffield (black), Göteborg (grey) and Wrocław (white). See text for further details

all three cities (yellow unbanded, mid-banded and many-banded (including trifasciate), and the same

DISCUSSION

Genetic differentiation among *C. nemoralis* populations is heavily influenced by their slow movement and poor powers of active dispersal. While local differences in selection can create differences in genetic composition over distances of only a few tens of metres (OŽGO 2008, 2011), there are other patterns of microgeographical variation that reflect founder effects and the common origin of adjacent populations (CAMERON & DILLON 1984). Such patterns are also found in molecular variation (ARNAUD et al. 1999, BELLIDO et al. 2002, SCHWEIGER et al. 2004). They are reflected in distance decay in genetic similarity. Both selection and the sources of existing pop-

Table 7. Values of F_{ST} estimated from morph frequencies and corrected for sampling error, together with the values estimated by bootstrapping and the associated standard deviations. Values of F_{ST} for Sheffield and Wrocław are taken from CAMERON et al. (2009). * – this figure relates to punctate shells, present in Sheffield but not elsewhere in any numbers. Trifasciate shells are similarly very rare in Sheffield. Data for Skåne, based on only eight samples, comes from unpublished material of R. COX and R. CAMERON

	Yellow	Brown	Un-banded	Mid-banded	Trifasciate
F_{ST} Göteborg	0.212	0.247	0.302	0.277	0.290
Estimated mean of F_{ST}	0.209	0.224	0.297	0.274	0.288
Estimated SD of F_{ST}	0.033	0.109	0.040	0.038	0.036
F_{ST} Sheffield	0.207	–	0.350	0.284	0.238*
F_{ST} Wrocław	0.089	–	0.092	0.123	0.111
F_{ST} Skåne	0.057	0.110	0.076	0.029	–

Table 8. The proportions (%) of samples visibly monomorphic at each locus considered in this study and in Sheffield and Wrocław (data from CAMERON et al. 2009). All three indicates samples monomorphic for colour, presence or absence of bands and for midbanded

Monomorphic	Göteborg	Sheffield	Wrocław
Samples	84	107	73
Colour	4.8	5.6	0.0
Banding	34.5	53.3	0.0
Mid in banded	17.8	28.0	9.6
00345 in banded	10.7	–	8.2
All three	0.0	2.8	0.0

combinations for pink). In all cases, samples from Göteborg resemble those of Sheffield rather than those from Wrocław. Table 7 also shows estimates of F_{ST} for a very limited set of populations from Skåne, an area thought to have been occupied for several centuries. These values resemble those of Wrocław.

ulations may be involved in particular cases (JONES et al. 1980, CAMERON & PANNETT 1985, OŽGO & KINNISON 2008).

Such patterns can be detected even in areas with long-established and relatively continuous populations (CAMERON & PANNETT 1985). However, they are most evident in areas where populations have been restricted to a few isolated refugia in the past and have subsequently spread (CAMERON & DILLON 1984), or in areas that have recently been colonised, usually as a result of accidental transport by humans followed by limited local active dispersal (CAMERON et al. 2009). In the former case areas of several km²

may contain sets of populations with very similar and often extreme morph frequencies, the “Area Effects” of CAIN & CURREY (1963). In the context of urban colonisation, such effects are missing, and the pattern of differentiation is more diffuse, reflecting multiple cases of passive dispersal and local spread and the degree of population continuity (CAMERON et al. 2009).

Populations of *C. nemoralis* in Göteborg show a pattern of local differentiation that shows no evident relationship to habitat or to the presence or absence of a similar species. Although there is a latitudinal influence on overall genetic similarity, perhaps reflecting sources of colonisation, there are no patterns resembling “Area Effects”, where large numbers of nearby populations have near-identical and often extreme morph frequencies. The pattern is mainly of very local trends for some but not all morphs to have similar frequencies in populations that are close to one another. The differentiation among populations is strong: many morph frequencies span nearly the whole range from 0–100% and values of F_{ST} are high (see below).

In these respects, populations of *C. nemoralis* in Göteborg resemble those studied in Sheffield much more than those in Wrocław, the two cities sampled by CAMERON et al. (2009). The degree of differentiation was less marked in Wrocław than in Sheffield and populations there were more polymorphic. These differences between the two could be related both to the history of the species in each and the degree of interconnectedness among populations; there was evidence that Wrocław had been occupied for longer, and had more continuous populations. In the case of Sheffield, the species had spread mostly in the previous twenty years. A priori, the pattern shown in Göteborg can be interpreted in the same way as for Sheffield: the very recent spread by accidental transport of small numbers by humans followed by some very limited active dispersal from the places in which snails were dropped. There is no doubt that the species has spread rapidly in the city in the last twenty years, and the contrast with areas where *C. nemoralis* has been established for many years (often centuries) is marked (CAMERON et al. 2009); it seems to hold even in a comparison with populations from Skåne in the extreme south of Sweden (Table 7).

There is, however, a much better historical record of *C. nemoralis* in Göteborg than in Sheffield and Wrocław, where there were very few samples available other than those made by CAMERON et al. (2009) during their studies from 2005 to 2008. This record indicates that the history of *C. nemoralis* in the city is not a simple one of spread from some initial point of introduction, with variation among populations generated by founder effects and genetic drift. The earliest records are characterised by very high frequen-

cies of yellow shells; these decline with time and in recently sampled populations the median value is less than 50%. Leaving aside possible scoring problems, there has either been selection against yellow sustained over a long period, or recent populations originate from sources other than those involved in the early samples. Temporal trends in the frequency of yellow shells across the geographical range of the species are unclear; SILVERTOWN et al. (2011) did not find any significant changes over time over the whole range. COOK (2014), however, detected an increase in yellow in some habitats within Great Britain and some local studies using accurately relocated sites have also shown increases over the last 50 years (CAMERON & COOK 2013, CAMERON et al. 2013). OŹGO & SCHILTHUIZEN (2011) showed an increase in yellow effectively unbanded. These changes have been attributed to rising mean temperatures over the period. The trend, where it has been detected, is thus in the opposite direction to that seen in Göteborg. As SILVERTOWN et al. (2011) have shown, the frequency of yellow shells decreases northwards over the range of the species and the modern median frequency in the city is within the range expected, whereas the early samples are discordant. This does suggest a different and perhaps less distant source or sources for modern populations.

One feature common to *C. nemoralis* populations in all three cities is the lack of variation with habitat. While this may reflect in part the difficulties in classifying the habitats, it is at first sight surprising, given that a number of studies have shown such variation even among recently established populations or habitat types (OŹGO 2011, OŹGO & BOGUĆKI 2011, CAMERON et al. 2013). In Wrocław, shaded habitats were mostly rather transitory, but both Sheffield and Göteborg contain some ancient woodland. Again, it suggests that colonisation of some habitats is very recent, and that adjacent populations in different habitats may have different origins. The lack of any correlation between members of a pair of shaded and open habitats (usually less than 1 km apart) supports this suggestion. The evidence from the studies mentioned above suggests that if populations survive for several generations, the effects of selection ought to become apparent.

This study of a third set of urban *C. nemoralis* populations reinforces the case made by COOK (1998) that this variation in *C. nemoralis* was strongly influenced by migration and gene flow, and in particular that the leptokurtic transport of individuals (some travelling much greater distances than possible by active dispersal) helped to maintain the polymorphism, which is found in nearly all populations. Similar patterns are seen in more rural areas where the evidence suggests that the species has spread recently (CAMERON et al. 2011, POKRYSZKO et al. 2012). As OŹGO (2011)

has also pointed out, the species is hermaphrodite, has multiple matings and long term allosperm storage. A single multiply-mated individual can carry a considerable proportion of the population's genetic variation at these loci, even when some alleles are at low frequency. Founder Effects do not have to result in monomorphic populations, but they can generate great variation among populations within a small area.

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APPENDIX

Appendix Table 1a. Locations and scores of polymorphism for all samples of *Cepaea nemoralis* used in this study and held in the Göteborg Natural History Museum and that of MEEUSE (1968, asterisked) samples in the museum were scored by TED VON PROSCHWITZ in 2014. Fuller details of locations and minor banding variants are available as a digital archive from the Göteborg Natural History Museum at www.gnm.se/cepaea. The samples are arranged by date. See text for shell colour and banding categories. Note that only samples of ten or more shells made from 1990 onwards were used in formal analyses.

Longitude (°E)	Latitude (°N)	Year	Collector	Total shells	Morphs								
					P0	P mid	P tri	P many	Y0	Y mid	Y tri	Y many	B0
11.9489	57.6969	1850	A. W. MALM	2	0	0	0	0	0	0	2	0	0
11.9489	57.6969	1873	EKEBERG	20	0	0	1	0	0	0	19	0	0
11.9489	57.6969	1886	K. A. ANDERSSON	22	0	0	0	0	0	0	8	14	0
11.9489	57.6969	pre 1900	ANONYMOUS	25	0	0	0	0	0	0	4	21	0
11.9489	57.6969	pre 1900	ANONYMOUS	28	0	0	0	0	0	0	14	14	0
11.9891	57.7094	1886	K. A. ANDERSSON	16	0	0	0	0	0	0	7	9	0
n/a	n/a	pre 1900	ANONYMOUS	6	0	0	0	0	1	1	2	2	0
12.0135	57.7210	1922	H. LOHMANDER	2	0	0	0	0	0	1	1	0	0
12.0284	57.7328	1922	H. LOHMANDER	1	0	0	0	0	0	0	0	1	0
12.0135	57.7210	1951	H. W. WALDÉN	1	0	1	0	0	0	0	0	0	0
11.9723	57.6742	1964	H. W. WALDÉN	1	0	0	0	0	0	0	0	1	0
11.9316	57.6258	1967	A. D. G. MEEUSE*	81	33	2	0	25	0	3	0	18	0
12.0226	57.7026	1975	T. VON PROSCHWITZ	1	0	0	0	0	0	1	0	0	0
12.0171	57.7322	1975	H. W. WALDÉN	7	0	0	0	1	0	5	0	1	0
12.0284	57.7328	1975	H. W. WALDÉN	5	0	0	0	1	0	2	0	2	0
12.0410	57.7340	1975	H. W. WALDÉN	1	0	0	0	0	0	1	0	0	0
11.9884	57.8685	1976	H. W. WALDÉN	7	0	0	2	0	0	1	3	1	0
11.9495	57.6906	1977	H. W. WALDÉN	1	0	0	0	0	0	1	0	0	0
12.0135	57.7210	1977	H. W. WALDÉN	11	0	2	3	2	0	2	0	0	2
11.9901	57.7146	1977	HWV/ TvP	24	1	4	1	3	0	2	0	13	0
11.9504	57.6904	1977	T. VON PROSCHWITZ	1	0	0	0	0	0	1	0	0	0
12.0959	57.3775	1978	M. WESTBERG	2	0	0	0	0	0	0	1	1	0
12.1193	57.6633	1983	H. W. WALDÉN	1	0	0	0	0	0	1	0	0	0
11.9500	57.6897	1984	T. VON PROSCHWITZ	29	1	8	0	1	1	3	1	14	0
11.9665	57.6880	1984	T. VON PROSCHWITZ	18	7	7	0	0	0	2	0	2	0
11.9474	57.6317	1984	T. VON PROSCHWITZ	10	0	0	0	0	0	0	0	10	0
11.9908	57.6851	1985	T. VON PROSCHWITZ	1	0	0	0	0	0	0	0	1	0
12.0310	57.7152	1985	T. VON PROSCHWITZ	10	0	0	8	0	2	0	0	0	0
11.8605	57.7060	1985	T. VON PROSCHWITZ	10	0	0	0	0	0	0	0	10	0
11.9330	57.7075	1985	T. VON PROSCHWITZ	6	0	0	1	0	0	0	0	5	0
11.9901	57.7146	1985	T. VON PROSCHWITZ	23	0	5	0	0	0	2	1	15	0
12.0135	57.7210	1985	T. VON PROSCHWITZ	20	0	0	6	0	0	1	1	12	0
11.9442	57.6287	1990	I. & J. HOBORN	12	0	1	0	5	0	0	0	6	0
11.9565	57.6463	1990	T. VON PROSCHWITZ	2	0	1	0	0	0	0	1	0	0
11.9307	57.7545	1992	U. ANDERSSON	7	0	0	4	0	0	0	3	0	0
12.0773	57.7151	1993	M. FRANZON	31	0	3	0	13	0	1	0	14	0
11.8881	57.6333	1993	A. MAGNUSSON	4	1	0	1	2	0	0	0	0	0
12.0670	57.7219	1993	T. VON PROSCHWITZ	6	0	0	1	1	0	0	3	1	0
11.8926	57.6361	1993	I.-L. OLSSON	6	0	0	1	0	0	1	1	0	3
12.0690	57.7418	1994	G. ELVMYR	4	0	0	0	0	3	0	1	0	0
12.1201	57.6632	1994	H. W. WALDÉN	2	2	0	0	0	0	0	0	0	0
12.0734	57.7239	1994	A. CLAESSON	2	0	1	0	1	0	0	0	0	0
12.1196	57.6638	1997	H. W. WALDÉN	2	0	1	1	0	0	0	0	0	0
11.8909	57.6362	1997	B. NILSSON	10	1	0	2	2	0	1	1	3	0
12.0716	57.7406	1997	I.-M. WALLENBERG	2	0	0	0	1	0	0	0	1	0
12.0604	57.7241	1997	L. HIKENBERG	1	0	0	0	0	0	0	1	0	0
12.0207	57.7646	1997	T. VON PROSCHWITZ	5	0	1	0	3	0	1	0	0	0
12.0129	57.7618	1997	T. VON PROSCHWITZ	5	0	1	0	1	0	2	1	0	0
12.0542	57.7434	1997	G. MATHIASSEN	14	0	3	1	2	0	6	1	1	0



Appendix Table 1a continued

Longitude (°E)	Latitude (°N)	Year	Collector	Total shells	Morphs								B0
					P0	P mid	P tri	P many	Y0	Y mid	Y tri	Y many	
11.9161	57.7191	1997	H. JONSSON	3	0	0	0	1	0	0	0	2	0
12.1196	57.6638	1998	H. W. WALDÉN	1	0	1	0	0	0	0	0	0	0
11.9045	57.6966	1999	J. JEPSON	1	0	1	0	0	0	0	0	0	0
12.0151	57.7096	1998	Å. HOLM	41	1	10	6	1	5	7	2	2	7
11.9045	57.6966	1999	T. VON PROSCHWITZ	3	1	0	1	1	0	0	0	0	0
11.9028	57.6969	1999	T. VON PROSCHWITZ	3	1	0	1	1	0	0	0	0	0
12.1260	57.6545	2000	I. RHODIN	4	0	1	1	0	0	0	1	1	0
11.9330	57.7257	2000	L. BENDZ	5	0	0	0	2	0	1	0	2	0
12.0074	57.7614	2000	T. VON PROSCHWITZ	8	0	0	6	1	0	0	0	1	0
11.9067	57.6332	2000	T. VON PROSCHWITZ	1	0	1	0	0	0	0	0	0	0
11.9480	57.6908	2000	T. VON PROSCHWITZ	30	3	6	2	0	3	6	0	9	1
11.9524	57.6831	2002	T. NORDANDER	1	0	0	0	0	0	0	0	0	1
12.1191	57.6649	2001	H. W. WALDÉN	1	0	0	0	0	0	0	0	1	0
12.0388	57.6954	2002	G. ANDERSSON	31	5	1	2	2	12	0	3	6	0
12.0693	57.8088	2002	L. CARLSSON	4	0	0	0	1	0	0	0	3	0
11.8897	57.6335	2004	D. JÖNSSON- HEMMINGSSON	5	1	0	0	2	0	0	0	2	0
11.9850	57.6765	2007	T. VON PROSCHWITZ	16	0	2	3	5	0	0	2	4	0
12.0021	57.6949	2007	T. VON PROSCHWITZ	19	0	0	0	0	1	5	10	3	0
11.9005	57.7496	2010	T. VON PROSCHWITZ	23	0	1	8	0	0	2	9	3	0
11.9177	57.6361	2010	T. VON PROSCHWITZ	19	0	0	0	0	0	7	6	6	0
11.9304	57.6407	2010	S. GYLLENHAMMAR	3	0	0	3	0	0	0	0	0	0
12.0028	57.6738	2011	T. VON PROSCHWITZ	21	8	3	2	0	5	1	2	0	0
11.9537	57.6827	2012	T. NORDANDER	4	1	1	0	0	0	1	1	0	0
12.0408	57.7503	2012	T. VON PROSCHWITZ	21	0	3	0	10	0	0	0	8	0
11.6129	57.7578	2013	T. VON PROSCHWITZ	16	0	0	3	1	0	3	6	3	0
12.1742	57.7480	2013	T. VON PROSCHWITZ	22	1	9	8	0	0	2	2	0	0
11.8438	57.7123	2013	T. VON PROSCHWITZ	16	0	2	7	6	0	0	1	0	0
12.0388	57.6594	2013	G. ANDERSSON	53	10	5	5	14	13	2	4	0	0

Appendix Table 1b. Details of location and morphs of *Cepaea nemoralis* for samples of 10 or more shells made in 2012 and 2013 and scored in the field. C: 1 – *Cepaea hortensis* present, 0 – absent; H: 1 – woods and shaded habitats, 2 – open habitats. See text for shell colour and banding categories.

Record name	C	H	Longitude (°E)	Latitude (°N)	Total	Morphs								B0	B mid	B tri	B many
						P0	P mid	P tri	P many	Y0	Y mid	Y tri	Y many				
Norra Kyrkvägen 5	1	2	12.0517	57.6080	14	0	5	4	1	1	0	2	0	1	0	0	0
E6 1	1	1	12.0334	57.6293	34	0	2	18	6	1	0	2	5	0	0	0	0
Kärrahöjd 1	1	2	12.0227	57.6376	38	21	2	3	9	0	0	2	1	0	0	0	0
Aminogatan 3	1	2	12.0030	57.6410	50	4	0	22	23	0	0	0	1	0	0	0	0
Hulelycksgatan 69	1	2	12.0462	57.6410	118	1	0	69	36	0	0	4	4	4	0	0	0
Aminogatan 7	1	2	11.9985	57.6414	53	0	5	7	16	0	1	14	10	0	0	0	0
Aminogatan 9	1	2	11.9900	57.6429	44	13	2	20	1	0	0	8	0	0	0	0	0
AZ 3	1	2	12.0179	57.6442	33	3	2	7	6	0	0	4	11	0	0	0	0
AZ 1	1	2	12.0198	57.6443	125	9	3	15	38	7	1	24	28	0	0	0	0
Södra Neganväggsgatan 1	0	2	12.0059	57.6444	17	0	0	3	9	0	0	0	4	1	0	0	0
Pepparedsleden 1	1	2	12.0164	57.6449	26	13	0	3	0	0	0	4	2	4	0	0	0
AZ 2	1	2	12.0196	57.6451	257	82	2	16	54	0	1	22	80	0	0	0	0
Hulelyckan 2	1	1	12.0458	57.6460	82	9	0	49	24	0	0	0	0	0	0	0	0
Toftaåsgatan 1	0	2	11.9184	57.6466	43	9	7	9	8	1	4	4	1	0	0	0	0
Hälleflundregatan 1	1	2	11.8587	57.6480	54	0	1	19	23	0	1	7	3	0	0	0	0
Hulelyckan 1	1	1	12.0415	57.6485	182	7	0	57	60	10	0	30	18	0	0	0	0
Eklanda 1	0	1	11.9661	57.6514	110	13	11	11	22	4	5	8	28	8	0	0	0
Rygatan 1	1	2	12.0300	57.6549	69	7	1	23	8	8	0	14	8	0	0	0	0
Mölnåls kyrka 1	1	2	12.0104	57.6558	11	3	0	1	3	3	0	0	1	0	0	0	0

Appendix Table 1b continued

Record name	C	H	Longitude (°E)	Latitude (°N)	Morphs												
					Total	P0	P mid	P tri	P many	Y0	Y mid	Y tri	Y many	B0	B mid	B tri	B many
Samuel Norbergsgatan 1	1	2	12.0273	57.6579	19	3	0	3	1	0	1	8	3	0	0	0	0
Delbancogatan 1	1	2	12.0281	57.6595	36	1	2	9	11	0	5	4	4	0	0	0	0
Stensjön	1	2	12.0417	57.6608	27	5	0	0	2	15	0	0	5	0	0	0	0
Eduard Boyes Gata	1	1	12.0299	57.6616	63	17	4	8	0	0	7	22	5	0	0	0	0
Mölnålsvägen 1	0	2	12.0136	57.6627	17	0	0	16	1	0	0	0	0	0	0	0	0
Bifrostgatan 2	1	1	12.0078	57.6643	27	16	0	3	4	4	0	0	0	0	0	0	0
Bifrostgatan 1	1	1	12.0084	57.6645	12	1	0	0	0	4	0	1	6	0	0	0	0
Bifrost	1	1	11.9927	57.6648	71	4	0	11	9	0	2	16	25	4	0	0	0
Långedrag 1	1	2	11.8544	57.6674	82	0	0	3	60	0	1	0	18	0	0	0	0
Dirigentgatan	1	2	11.9218	57.6678	42	1	10	1	14	0	8	0	7	1	0	0	0
Ruddalen	0	1	11.9166	57.6693	69	0	23	19	24	0	0	1	2	0	0	0	0
Toltorpsdalen	1	3	11.9741	57.6760	48	7	6	2	27	3	1	0	2	0	0	0	0
Kallebäcksmotet 2	1	2	12.0029	57.6852	44	11	1	12	19	0	0	0	1	0	0	0	0
Älvsborgsbron 1	1	1	11.9021	57.6884	21	0	5	3	10	0	0	1	2	0	0	0	0
Kallebäcksmotet 1	1	2	12.0043	57.6889	163	0	103	23	6	0	24	4	3	0	0	0	0
Chalmersplatsen	1	2	11.9711	57.6897	10	0	7	0	0	0	2	0	1	0	0	0	0
Egnahemsvägen	1	2	11.9700	57.6913	13	8	0	3	1	0	0	1	0	0	0	0	0
Jaegerdorffsmotet 1	0	2	11.9130	57.6917	61	4	15	21	19	0	0	0	2	0	0	0	0
Delsjövägen 1	1	2	12.0074	57.6991	54	1	10	17	8	2	1	9	2	4	0	0	0
Alfred Wigelius väg	1	1	12.0179	57.7003	124	15	1	47	4	0	2	41	3	10	0	1	0
Delsjövägen 4	1	2	12.0174	57.7006	29	1	7	5	8	0	0	0	3	5	0	0	0
Örgryte Nya Kyrkan	1	1	12.0054	57.7024	82	1	13	17	9	0	14	16	10	2	0	0	0
Lille Munkebacks g	1	2	12.0250	57.7032	38	0	0	11	20	0	0	4	3	0	0	0	0
Anders Zornsgatan	1	1	12.0192	57.7053	79	0	2	30	6	0	5	15	1	10	4	6	0
Torp	1	1	12.0278	57.7073	54	0	3	0	13	0	10	0	28	0	0	0	0
Birkagatan 1	0	2	12.0228	57.7097	56	0	19	10	11	0	9	4	3	0	0	0	0
Ulfsparrgatan 1	1	1	12.0159	57.7108	75	1	13	9	13	0	6	12	9	11	0	1	0
Virginsgatan 1	1	2	12.0297	57.7109	28	0	4	0	0	0	10	11	3	0	0	0	0
Oakwood	1	1	12.0171	57.7114	55	1	4	11	6	0	5	10	9	8	1	0	0
Garden centre	1	2	12.0189	57.7124	60	4	16	7	3	1	15	7	2	5	0	0	0
Källtorpsgatan 1	0	2	12.0193	57.7128	115	0	27	4	5	0	56	9	10	4	0	0	0
Jewish Cem	1	2	12.0196	57.7131	64	5	14	3	2	1	26	6	3	4	0	0	0
Östra kyrkogård 1	0	2	12.0153	57.7132	10	0	0	1	1	0	0	1	0	7	0	0	0
Sanatoriegatan tram stop 1	0	2	12.0240	57.7139	67	0	12	23	4	0	13	13	2	0	0	0	0
Skansen Lejonet 1	0	2	11.9894	57.7141	55	0	7	3	12	0	12	6	15	0	0	0	0
Sanatoriegatan 1	0	1	12.0317	57.7142	49	1	5	1	8	1	20	10	3	0	0	0	0
Poppelmansgatan 1	0	2	12.0193	57.7154	12	0	0	4	2	0	0	4	2	0	0	0	0
Stobéegatan/ Övergårdsstigen 1	0	2	12.0310	57.7156	37	0	4	10	12	0	2	4	5	0	0	0	0
Solrosgatan tram stop 1	0	2	12.0249	57.7166	45	1	7	17	12	0	2	4	2	0	0	0	0
Härlandavägen 1	0	1	12.0091	57.7170	25	0	1	1	21	0	0	0	2	0	0	0	0
Goteborg	1	2	12.0200	57.7180	147	0	5	0	75	7	0	0	60	0	0	0	0
Jewish cem 2	1	2	12.0174	57.7188	36	0	2	6	5	0	2	5	10	6	0	0	0
Landerigatan 1	1	1	12.0130	57.7192	111	0	13	29	24	0	8	7	29	1	0	0	0
Härlanda gamla kyrka 1	0	2	12.0225	57.7198	85	0	14	6	30	0	4	2	29	0	0	0	0
Östra sjukhuset 2	1	1	12.0468	57.7204	79	0	4	8	36	0	2	9	20	0	0	0	0
Östra sjukhuset 1	0	2	12.0470	57.7208	81	1	1	7	36	0	0	4	32	0	0	0	0
Ribbas gata 1	0	1	12.0218	57.7226	120	0	21	10	10	0	20	36	23	0	0	0	0
Lilla Munkebäcksgatan 1	0	2	12.0208	57.7238	45	0	11	5	2	3	16	5	3	0	0	0	0
Partille 1	1	2	12.1082	57.7364	26	0	1	2	4	0	1	5	13	0	0	0	0