CEPAEA NEMORALIS (L.) ON ÖLAND, SWEDEN: RECENT INVASION AND UNEXPECTED VARIATION

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ABSTRACT: *Cepaea nemoralis* is a recently introduced species on Öland. Discounting an early and debateable record, the species has been recorded only in the 21st century, despite intensive earlier faunistic surveys. A recent survey has yielded records from the whole length of the island (137 km), but the majority of known populations are in its southern half, most particularly around the settlements of Mörbylånga, Gräsgård and Färjestaden. Populations are usually in anthropogenic habitats. Most appear small and isolated by less disturbed areas. Nearly all samples are polymorphic for both colour and banding morphs, and the variation among populations is low when compared with similar sets from other places where recent colonisation has occurred. There is no latitudinal variation in morph frequencies, nor is any spatial autocorrelation apparent. While a relatively uniform and rigorous selection regime could account for the patterns seen, a single initial introduction followed by transport of propagules large enough to minimise founder effects is also possible.

KEY WORDS: introduced species; *Cepaea nemoralis*; shell polymorphism; Öland; Sweden

INTRODUCTION

The polymorphic European land snail *Cepaea nemoralis* (L.) has become a "model organism" in the study of visible genetic variation within and among populations (OŻGO 2008, 2012, ROSIN et al. 2011, COOK 2017). These studies involve the famous shell colour and banding polymorphism (JONES et al. 1977, COOK 1998). The genetics of much of this variation is known, though that of minor variation in number of bands and of fusions among them remains undetermined (summary in JONES et al. 1977). Both within the natural range and elsewhere, numerous surveys at many scales have identified patterns of variation in which various selective agencies, are implicated, most significantly those caused by predation and climate (SILVERTOWN et al. 2011, CAMERON 2016).

There is, however, evidence that population history involving bottlenecks and founder effects influence morph frequencies. In more general terms, genetic drift may be significant both in influencing the amount of variation within populations and the magnitude of differences between them. The interaction of these processes is often complex, even within the natural range, within which there have been significant environmental changes (CAMERON & DILLON 1984, CAMERON & PANNETT 1985). The balance and interaction of these processes in relation to the circumstances of the populations enhances our understanding of evolution at the most basic level (OŻGO 2008, COOK 2017).

C. nemoralis is a species with a wide ecological tolerance. It is frequently abundant in very anthropogenic habitats, and it is easily spread accidentally, perhaps most often with horticultural products. Most evidently in the last three or four decades, it has been expanding its range both into urban areas previously too polluted to sustain it (CAMERON et al. 2009) and

more generally into largely anthropogenic and urban habitats to the north and east of its natural range (OŻGO 2005, CAMERON et al. 2011, PELTANOVÁ et al. 2012, POKRYSZKO et al. 2012, GHEOCA 2018, OŻGO et al. 2019, GURAL-SVERLOVA et al. 2020), extending as far east as Moscow (EGOROV 2018).

Sweden is thought to lie outside the original, natural range of *C. nemoralis,* although the extreme south, Skåne, has been occupied for several centuries (WALDÉN 1986). It was deliberately or accidentally introduced to a few places further to the north in the 19th century (CAMERON et al. 2014, CAMERON & VON PROSCHWITZ 2019), but remained restricted until late into the 20th century. Since then, it has spread not only from these sites, but has extended its range northwards. In 2013 it was found in Härnösand [62°38'N] (VON PROSCHWITZ 2015), and in 2020 as far north as in Umeå [63°49'N] (data from the Swedish Species Information Centre).

Studies on the shell colour and banding polymorphism of these recently established populations of *C. nemoralis* (cited above) have revealed patterns of variation that demonstrate the influence of founder effects or genetic drift, a product of long-distance transport followed by local dispersal, the latter certainly aided by human activity. The Swedish island of Öland had only one, disputed, record of *C. nemoralis* earlier than the 21st century, despite many intensive faunistic surveys. Populations are now known from the whole length of the island, though populations appear to be small and isolated from one another. We report here on surveys conducted over the last 10 to 15 years that reveal an unexpected pattern of variation somewhat discordant with patterns seen in other regions where the species is a recent arrival, and in particular in the cases of Göteborg (CAMERON et al. 2014) and the nearby island of Gotland (CAMERON & VON PROSCHWITZ 2019).

AREA STUDIED

Öland is a long, thin island in the Baltic Sea (137 km north to south, and 16 km across at its widest, centred on 56°40' north and 16°40' east) lying parallel to the eastern coast of mainland Sweden (Fig. 1A).

While containing the same Silurian limestone scenery as its northern neighbour Gotland, it is smaller (1,342 km² versus 3,183 km²), flatter (highest point, 55 m a.s.l. versus 82 m) and with a drier and warm-
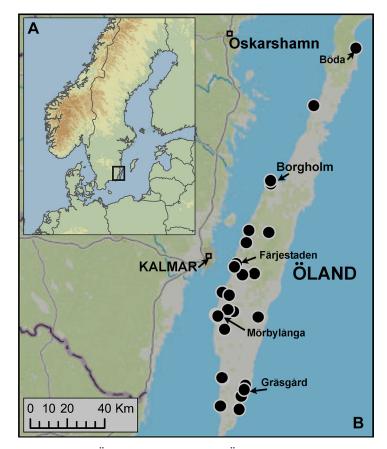

Fig. 1. Research area: A – the position of Öland; B – the island of Öland, showing the location of sampling sites used in the study

er climate (January mean temperature +0.7–0.9 °C versus −0.6 °C, July, 20.9–21.6 °C versus 17.9 °C, precipitation, 392–420 mm annually versus 525 mm on Gotland). Göteborg, much further west, is both cooler in summer and wetter than either island, with lower summer temperatures, less sunshine and double the precipitation of Öland. Populations of *C. nemoralis* so far discovered span the whole length of the island (Fig. 1B).

EARLIER SURVEYS, MATERIAL AND METHODS

All the samples of *C. nemoralis* used for analysis are held in the Natural History Museum of Göteborg (Appendix). Prior to surveys in the 21st century there is only one authenticated record of *C. nemoralis*, a sample of three yellow unbanded shells from the island's capital, Borgholm, collected in 1895 by an unknown person. It is not recorded in the comprehensive faunal account of WESTERLUND (1884), nor in his overview of the North European mollusc fauna (WESTERLUND 1897) and his supplement to the original 1884 fauna (WESTERLUND 1904). Hans Lohmander (1896–1961), who was curator at the Göteborg museum, performed extensive fieldwork on Öland in 1924, 1928, 1937, 1939 and 1941 (LOHMANDER 1937, 1938, 1940). He examined 943 localities on the island, none of which yielded *C. nemoralis* (VON PROSCHWITZ 1999). Further evidence for its absence in the first half of the 20th century comes from SCHLESCH (1937), reporting on his collecting experiences the previous year: "*C. nemoralis* fehlt gänzlich" (totally absent).

There were no surveys on the same scale in the second half of the 20th century, but one of us (T. von Proschwitz) had visited and sampled on the island frequently from 1979 onwards. The first occasion on which he found *C. nemoralis* was in 2005 in the nature reserve Mysinga alvar near Resmo (VON PROSCHWITZ 2007). Unknown at the time, there was an earlier record made by G. Schmid in 2001, in a garden in Fäjestaden; this record, and another made by T. von Proschwitz during the spring meeting of the German Malacological Society (Frühjahrstreffen der DMG) 2007 were published in the report from that meeting (VON PROSCHWITZ 2014).

The only record notionally from the 20th century is that of JAECKEL (1962): "Ins. [Inseln] Öland und Gotland" [Islands Öland and Gotland]. The basis on which he made this statement is not known, though he may have been aware of the 1895 record. WALDÉN (1966) refuted Jaeckel's claim ("nicht auf Öland"), and further doubted the authenticity of the locality for the 1895 record (in litt. to T. von Proschwitz).

With the exception of the 1895 record, all samples were made and scored by T. von Proschwitz. Scoring of colour and banding morphs followed the system used by JONES et al. (1977) with a full tally of bands present and the extent of fusions among them. We have used the standard categories of yellow, pink and brown for shell colour; for banding, we have used four standard categories of unbanded (00000), mid-banded (00300), trifasciate (00345) and many-banded (12345), with minor variants ascribed to the most appropriate category. Thus, for example, 00045 shells were allocated to the trifasciate class, and 10345 to the many-banded class. We have not considered the occurrence of fused bands as information about this is often absent from other studies, and is not always presented in a standard manner. Full details are, however, available from the Natural History Museum of Göteborg.

For analysis, only the 29 samples containing 10 or more scoreable shells were used. In two cases (Appendix) repeat samples from the same site have been combined. All were made in the 21st century. We did not attempt to classify habitats by shading; they were all from rather heterogeneous anthropogenic sites. Frequencies of the colour morphs and of unbanded shells were calculated relative to the whole sample; 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). We used a modified version of F_{ST} (WEIR & COCKERHAM 1984) as a measure of variation among samples; it was corrected for sampling error and used morph- rather than allele frequencies, following CAMERON et al. (2009). Moran's I was used to test for spatial autocorrelation (CAMERON et al. 2014).

RESULTS

The Appendix gives details of the location and composition of all 29 samples used. Site locations are shown in Figure 1B. With only a few exceptions, snails were hard to find; mean sample size was 19.7 scoreable shells and the median only 14. All major morphs were present on the island, and most populations were polymorphic at each locus (Table 1). Brown shells were present at only five sites and at

Table 1. Basic data on the frequencies of the major morphs in 29 samples of *C. nemoralis* from Öland

Frequency [%]	Yellow	Unbanded	Midbanded in banded	Trifasciate in many banded
Mean	41.9	51.6	61.6	32.7*
Median	43.6	53.8	63.6	33.3*
Range	0–85.7	11.8–81.3	0–100	0–100*
Monomorphic	Colour	Bands +/−	Mid +/−	Tri +/−
Number of populations	1	0	9	11*
% of populations	3.4	0	31.0	47.8*
Median sample size	14	14	7	4

* – many-banded shells were present in only 23 populations. Values relate only to those populations.

Table 2. Values of F_{ST} corrected for sampling error and modified following Cameron et al. (2009) for major loci on Öland and in other studies referred to in the text. Göteborg and Sheffield are recently colonised, with isolated populations. Wrocław has been occupied for longer and at greater density, while the area of central England (using data from Silvertown et al. 2011, as also presented in Cameron & von Proschwitz 2019, open habitats only) contains well established populations within the natural range. Gdańsk represents an intermediate condition

F_{ST} (corrected)	Öland	Gotland	Göteborg	Sheffield	Wrocław	Central England	Gdańsk
Yellow	0.107	0.037	0.212	0.207	0.089	0.116	0.165
Unbanded	0.071	0.271	0.302	0.350	0.092	0.096	0.185
Mid in banded	0.254	0.249	0.277	0.284	0.123	0.137	0.169
Trifasciate	0.248	n/a	0.290	n/a	0.111	n/a	n/a

low frequency. There are no significant associations between any morph and latitude or longitude. Further, there are no signs of any spatial autocorrelation: values of Moran's I not only lack significance, but all values at all distances are close to zero (data not shown). Similarly, there are no among-sample associations between morphs, and linkage disequilibria between the colour and banding loci are slight, and are equally distributed in opposite directions. Values of F_{ST} for colour and for unbanded are low relative to values obtained in other studies on introduced populations (Table 2; see discussion below). Those for mid-banded and trifasciate are higher, but given the very small number of shells on which they are based (medians of seven and four shells per sample, respectively) they may be less than reliable even with sample size correction.

DISCUSSION

On the evidence available, the populations of *C. nemoralis* recorded on Öland are of very recent origin, most probably stemming from introduction very late in the 20th century. While we cannot absolutely discount the record of 1895, it is notable that intensive surveys over nearly 50 years thereafter failed to yield more records, in contrast to the situation in Göteborg (Cameron et al. 2014) or on Gotland (Cameron & von Proschwitz 2019), where 19th century records were followed by further observations, even if numbers and sites remained limited until the late 20th century.

This pattern of late 20th and then 21st century spread is found repeatedly as the species continues to advance northwards in Sweden. It is paralleled by rapid contemporaneous expansion into urban and anthropogenic habitats elsewhere, as documented in the introduction. Arrival and spread on Öland is very much in accord with the general trend.

The pattern of variation in *C. nemoralis* on Öland, however, does not conform to that usually found among such recent, colonising populations, where F_{ST} is high, and spatial autocorrelation at small scales is often strong (e.g. Cameron et al. 2014). Despite small sample sizes, and the apparent isolation of individual populations, most remain polymorphic at the major loci (Table 1). The range of among population variation, as estimated by F_{ST} (Table 2) is limited, at least for the more reliable estimates for shell colour and the presence or absence of bands. They resemble values obtained from central England, where selection for crypsis is well-documented and populations are long-standing and frequently continuous, or from urban populations with greater connectivity and large population sizes such as Wrocław (Cameron et al. 2009). The contrast with Göteborg on all these measures is striking, as is the lack of spatial autocorrelation, which was manifest in the distribution of

brown shells and the frequency of banding variants in the city (Cameron et al. 2014), and has also been found frequently elsewhere, even in areas within the natural range, and in stable habitats (Cameron & Pannett 1985, Pokryszko et al. 2012).

The repeated patterns of variation in freshly colonised regions (high values of F_{ST} and strong spatial autocorrelation over short distances) have been related to long distance transport of small numbers, with later small-scale migration or transport, involving founder effects and genetic drift, with minimal gene flow between populations. There is no evidence that the process of colonisation on Öland is in any way unique, while the pattern of variation is very different. While the limited number of samples, and their small size enforce caution, the striking difference between Öland and most other recently colonised regions suggests two possible explanations. Assuming a single introduction event, then if actual population sizes remain large and the numbers transported to new sites on the island are adequate, deviation from the original composition will be modest in the absence of differing selection pressures among sites. While a single introduction event is plausible, sampling to date gives no grounds for assuming large or interconnected populations (nor, conclusively, to reject the idea). The limestone bedrock may indeed facilitate dispersal, but the snail has not been found in sites away from human disturbance.

The other possibility is that variation is constrained by selection of a kind that is relatively uniform across the island. In this context, we can note that while the median frequencies of colour morphs differ only slightly among the nearest comparable surveys (Table 3), the frequency of unbanded and effectively unbanded shells is significantly higher on Öland than elsewhere in the region, and remarkably uniform across samples (F_{ST} for this genetically heterogeneous category is only 0.062, cf. Table 2). The island is drier, sunnier and warmer in summer than Gotland, and much more so than Göteborg or Gdańsk. Öland, indeed, resembles locations at the southern limits of the snail's natural distribution in terms of sunshine and precipitation, though not summer temperatures.

The evidence that such environmental conditions favour such effectively unbanded shells (excluding

Table 3. The mean frequencies of yellow, unbanded and "effectively unbanded" (top two bands missing) shells in samples of *C. nemoralis* from Öland, and in the three nearest regions in which surveys have been carried out. Gotland is c. 70 km distant, Göteborg and Gdańsk ca. 320 km distant (west and south respectively). Data from Cameron et al. (2011), Cameron et al. (2014) and Cameron & von Proschwitz (2019). Figures for Gdańsk refer to open habitats only

	Öland	Gotland	Göteborg	Gdańsk
Yellow	41.9	54.6	38.1	45.5
Unbanded	51.6	29.6	5.6	29.0
Effectively unbanded	87.7	64.6	63.8	69.0

brown shells) is equivocal; in some regional comparisons, the frequencies of effectively unbanded shells in open habitats are higher in the sunnier, hotter and drier regions (Lamotte 1966, Arnold 1969), and there is some evidence that the lack of bands on the upper part of the shell, reflecting more sunlight, moderates temperature increase when exposed (Emberton & Bradbury 1963, Lamotte 1966). More generally, dark shells, with bands as a darkening feature as well as shell colour, may reach higher equilibrium temperatures in sunlight (Heath 1975, Tilling 1983). In broader comparisons, however, such associations are far from universal (Jones et al. 1977), and the many other factors affecting morph frequencies have obscured any general trend that might occur when the whole range is considered (Silvertown et al. 2011). Our purpose is not to make a claim, but to point to possibilities, given the unusual pattern of variation in this particular set of introduced and expanding populations. Further work will provide more clarity, and the data are available as a basis for such studies.

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APPENDIX

Samples of *Cepaea nemoralis* (L.) made on Öland. Longitude and latitude given in DDM. For the date of sampling, two sites were sampled on more than one occasion

Longitude	Latitude	Date	1st	N	P0	P3	P tri	P5	Y0	Y3	Y tri	Y5	B0	Locality
16°39.36'	*56°52.80'*	*1895*		*3*					*3*					*Borgholm*
16°28.38'	56°32.16'	2005–2020	2005	14	1	1			6	3	1	2		Resmo, 750 m WNW of p.39.22
16°27.06'	56°34.80'	30.06.2020		11	1		1	2	6		1	1		Vickleby, 500 m WNW of the church
16°26.82'	56°39.90'	01.07.2020	2001	11	3				2	3		3		Torslunda, Färjestaden, Paradisgatan
16°23.46'	56°31.44'	30.06.2020		29	4	4	1	2	9	5	2	2		Mörbylånga, Trollstigen
16°34.38'	56°38.22'	01.07.2020	2018	10		3		1	2	3	1			Torslunda, 400 m NNW of Hildeborg
16°23.88'	56°31.20'	2015–2020	2015	87	15	8	2	8	35	8	1	8	2	Mörbylånga, cemetery
16°26.64'	56°32.46'	28.06.2020		18	5	1	1		8	1		1	1	Resmo, cemetery
16°30.00'	56°16.50'	01.07.2020	2012	13	4	2			3	2		2		Gräsgård, Össby, in the harbour
16°39.06'	56°52.98'	24.06.2020		28	8			6	9			5		Borgholm, cemetery
16°35.46'	56°31.26'	30.06.2020		14	4	2		2	5			2		Stenåsa, 870 m W of St. Brunneby
16°31.44'	56°19.68'	01.07.2020	2013	12	4	2			3	2	1			Gräsgård, Gammalsby, 350 m S of the crossroad
17°03.78'	57°13.86'	01.07.2020		13	7				2	4				Böda, Mellböda, recycling centre
16°24.96'	56°21.54'	01.07.2020	2011	16	4	3		2	3	2	1	1		S. Möckleby, 600 m NW of the church
16°29.82'	56°16.56'	01.07.2020	2012	16	4	4		1	2	3	2			Gräsgård, Össby, in the village
16°23.82'	56°31.44'	30.06.2020	2015	39	9	8	3	2	9		6	2		Mörbylånga, Drömstigen
16°25.32'	56°21.36'	29.06.2020		12	6	1			2	3				S. Möckleby, cemetery
16°30.90'	56°38.04'	28.06.2020		39	10	12		1	2	8	5	1		Torslunda, cemetery
16°32.04'	56°43.14'	28.06.2020		17	2	5	3	1		2		4		Glömminge, cemetery
16°28.98'	56°39.84'	30.06.2020		17	5	4		2	4	2				Algutsrum, Mölltorp, Basilkagränd
16°38.52'	56°44.76'	27.06.2020	2007	12	4	4			2	2				Långlöt, Ismantorp's fortress
16°23.16'	56°31.68'	27.06.2020		17	6	3	1		3	1		1	2	Mörbylånga, 770 m E of the guest harbour
16°51.66'	57°40.80'	25.06.2020	2014	31	9	8		4	8			1	1	Persnäs, Sandvik, 1 km NNE of the pire
16°32.82'	56°45.06'	30.06.2020	2011	14	2	8			2			2		Glömminge, 200 m ENE of Rosti
16°39.18'	56°52.44'	26.06.2020	2015	16	11			1				4		Borgholm, Åkerhagen, Johan IIIs väg
16°31.74'	56°20.34'	01.07.2020	2017	17	7	6			1	3				Gräsgård, Selby, 850 m NNE of the crossroad
16°25.74'	56°29.34'	29.06.2020		11	5	2			2				2	Kastlösa, cemetery
16°25.08'	56°35.22'	01.07.2020	2012	13	2	5	4			2				Vickleby, Bejershamn, 700 m NNE of Fröbygårda
16°30.48'	56°18.60'	29.06.2020		12	7	4			1					Gräsgård, cemetery
16°24.48'	56°17.04'	29.06.2020		12	7	2		3						Ventlinge, cemetery

1st – indicates date of first record for the site if prior to sampling; N – number of shells scored; P – pink shell colour; Y – yellow; B – brown; 0 – unbanded; 3 – midbanded; tri – 00345; 5 – many bands with at least one of the upper two present. Data with full details of band variation, including fusions, is available from the Göteborg Museum of Natural History. The 1895 sample (in italics) is not included in analyses.