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Change and stasis in urban populations of the land snail *Cepaea nemoralis* over five to six generations

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Repeat surveys of the shell colour and banding polymorphism in populations of the land snail *Cepaea nemoralis* in the cities of Sheffield (UK) and Wrocław (Poland) and in its surrounding settlements were made after a 13-18 years interval. In all three cases, a substantial proportion of sites had been destroyed by development (18-30%) and a similar proportion no longer held the species, despite being apparently suitable; up to 50% of populations had disappeared. Overall, the pattern was one of stasis in morph-frequencies, and of little change in the range of variation as estimated by a modified version of F_{st}. There were, however, substantial changes in some populations, not consistent in direction, but larger than expected from sampling error. While there was tenuous evidence for selection against yellow shells, the large changes are attributed to bottlenecks, founder effects, and possible local extinction and recolonisation. Urban populations are often transitory and the results are contrasted with those from an area of long-term habitat stability and population connectivity. Newly established and sometimes transitory populations offer opportunities to study underestimated aspects of evolutionary processes.

Key words: polymorphism, shell, bottlenecks, recolonisation, selection.

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The land snail *Cepaea nemoralis* (L.) is well-known for the many studies of its shell colour and banding polymorphisms; there are good reviews in Cook (1998, 2007, 2017), and there are brief accounts in Ożgo (2008) and Cameron (2016). The characters involved are entirely hereditary, and it has been possible to find evidence for selection relating to shade and/or crypsis in long-established populations in stable habitats (Cameron & Pannett 1985; Cameron *et al.* 2013), as well as in transitory populations at the margins of the species range, where selection can be particularly strong (Ożgo & Kinninson 2008; Cameron *et al.* 2011; Ożgo 2011; Ożgo & Bogucki 2011). There are also correlations with climate (Silvertown *et al*. 2011). In some cases, however, the pattern of variation does not correspond to manifest environmental differences among populations. It may reflect a past history of genetic bottlenecks in refugia, and subsequent expansion (Cameron & Dillon 1984), the classic area effects of Cain & Currey (1963) or long-distance, passive dispersal followed by more local spread (Ożgo *et al.* 2019). It might also reflect recent expansion into previously unoccupied places. This spread has happened on a large scale in Eastern, far Northern and Central Europe (Dvořák & Honěk 2004; Ożgo 2005, 2012; Peltanová *et al.* 2012; Egorov 2018; Gheoca 2018; Cameron & von Proschwitz 2019, 2020; Balashov & Markova 2021; Gural-Sverlova & Kruglova 2022), but also in cities within the natural range where industrial pollution had previously made the environment unsuitable (Cameron *et al.* 2009). The spread is mainly passive and often related to the distribution of horticultural products. Occasionally, it originates from known, deliberate introductions in North America as well as Europe (Ożgo 2005; Whitson 2005; Bergey *et al.* 2014; Cameron *et al.* 2014; Örstan & Cameron 2015; Gural-Sverlova *et al.* 2021).

There are now a number of studies of urban populations of both *C. nemoralis* (Kerstes *et al.* 2019) and its congener *C. hortensis* (Gheoca *et al.* 2019). The patterns of variation discovered generally reflect a number of founding effects, in which the sources or constitution of original introductions are sometimes, but not always, known. Among these studies, those of Cameron *et al.* (2009) and Pokryszko *et al.* (2012) examined variation in the cities of Sheffield (UK) and Wrocław and its surrounding settlements (Poland). Nearly all populations from Sheffield were less than 40 years old at the time of the first survey (a product of cleaner air), as were those around Wrocław, the area being only recently colonised. In Wrocław itself, however, there is a longer history of occupation, and its spread has been aided by the massive destruction inflicted in the closing weeks of World War II, and the resultant increase in wasteland within the city. Correspondingly, populations were more connected and alike, although there was no evident relationship to habitat. Founding events were indicated by microgeographical patterns of similarity in both studies.

Changes and stasis over time, in relation to climate or habitat, have been detected in a number of studies (e.g. Silvertown *et al.* 2011; Ożgo & Schuilthuizen 2012; Cameron & Cook 2013). Such repeat surveys are a powerful tool in understanding the evolutionary dynamics of the polymorphism and the roles of selection, drift and founder effects (Ożgo 2014; Ożgo *et al.* 2017). We thus decided to resurvey as many populations as possible used in the studies of Cameron *et al.* (2009) and Pokryszko *et al.* (2012), to see if any changes had occurred that might indicate causation.

Material and Methods

Details of the districts in which samples were made are given in Cameron *et al.* (2009) and Pokryszko *et al.* (2012). In Sheffield, where resampling was possible over two years, all but two sites in which more than 20 shells of *C. nemoralis* were found were visited; the two being a garden in which introductions had been made, and a site apparently suitable but no longer accessible. In Wrocław and its surroundings (villages), around half the sites originally surveyed could be visited. In both cases, the sites visited appeared to be a fair sample, differing little in original morph-frequencies from the means for the survey as a whole.

Site locations in the original surveys for Sheffield and Wrocław were marked on detailed town plans or 1: 25,000 topographical maps. Those in the region around Wrocław were located by GPS. While there is room for error in relocation, it is small; almost always less than 50 m. Habitats were recorded on a four-point scale: woodland, 1; scrub, 2; mixed/intermediate, 3; open, with grassland or herbs but no woody plants, 4. The majority of sites fell into category 3 – mixed/intermediate. We did not assess the exact proportions of cover within such sites; there was often great variation within each. Sites were no more than 400 m^2, nor longer than 30 m in a linear habitat such as a hedge or roadside verge. Sampling in Sheffield was carried out by R.A.D.C. alone on both occasions. Samples from Wrocław were made by R.A.D.C and the late Beata M. Pokryszko in the first survey; they and M.O. sampled in the region around. M.O. and E.K.-K. carried out the resurvey in both Polish regions.

Shells were scored for genetic morphs following Cameron *et al.* (2009): shell colour: yellow, pink or brown; banding: unbanded, mid-banded (00300), and many-banded (mostly 12345). In Poland, trifasciate (00345) was also scored, while in Sheffield the punctate condition was scored in many-banded shells. Minor variants were allocated to the nearest match among these categories; they were uncommon. Only samples of at least 20 shells were used in analysis. Live snails were scored in the field and returned to the site.

A paired sample t test was used to detect any systemic change in frequencies over the period. The direction and magnitude of change in morph-frequencies were used both to indicate potentially significant changes and any overall shift. Variation among sites was examined using a modified version of F_{st}, corrected for sample size and using morph- rather than allele-frequencies (Cameron *et al.* 2009). Its function here is to examine variance relative to the maximum possible at the given mean frequency, as when a mean frequency is very high or low, the maximum variance is constrained. It serves no formal genetic function as an inbreeding coefficient (Wright 1978).

Results

Of the sites searched in each region, up to 50% no longer held *C. nemoralis* (Table 1). Some sites had been destroyed as habitat, while others appeared suitable, but yielded no snails, or a handful of long empty shells. In general, *C. nemoralis* was much harder to find in the resurvey, and in Sheffield the majority of shells were empty at most sites. Repeated sampling to reach 20 shells was needed in many cases.

The composition of original and later samples for all three areas is given in the Supplementary Material (SM.01-SM.03), together with their location and habitat. Overall, there has been little change in morph-frequencies, or in the amount of variation among populations (Table 2), although F_{st} values are generally slightly lower in the second sampling. Paired sample t tests for any directional change are consistent in showing no significant change. The

Table 1

Numbers of sites sampled in the original surveys, numbers searched in the second surveys and the outcomes of the searches

Sites	Sheffield	Wrocław	Villages
Original survey	107	73	105
Searched	105	38	56
Sampled	66	19	33
Destroyed	19	10	17
No snails*	21	9	6
% destroyed	18.0	26.3	30.3
% no snails	20.0	23.7	10.7
% total loss	38.0	50.0	41.0

*A few of these sites revealed a very small number of long--dead shells

Table 2

Mean frequencies of yellow, unbanded, mid-banded and (for Sheffield) punctate, and (for Polish areas) trifasciate specimens, together with the corrected estimates of F_{st} as defined in the text. Note that the frequencies of mid-banded, punctate and trifasciate shells are based on those in which the characteristic can be observed. The numbers involved are given as medians for the purpose of calculating the sampling error. Brown shells were present in a few samples; while brown banded shells have been allocated to the appropriate pink shell classes

Sites/ Morphs	Median	Mean Yellow	F_{st} Yellow	Mean Un-banded	F_{st} Un-banded	Median Banded	Mean Mid-banded in Banded	F_{st} Mid-banded in Banded	Median Many-banded	Mean Punctate in Many-banded	F_{st} Punctate in Many-banded
Sheffield N = 66											
Original	52.5	55.9	0.227	8.7	0.368	48	15.4	0.311	41	24.8	0.198
Repeat	46	50.5	0.206	10.5	0.277	41	18.7	0.297	33	26.1	0.192
Difference		-5.4	-0.021	+1.8	-0.090		+3.3	-0.014		+1.3	-0.006
Wroclaw N = 19										Trifasciate in Many--banded	
Original	109	64.4	0.092	37.0	0.115	71	16.4	0.099	62	20.6	0.145
Repeat	54	62.1	0.068	40.2	0.069	34	16.5	0.158	25	21.1	0.114
Difference		-2.3	-0.024	+3.2	-0.046		+0.1	0.059		+0.50	-0.031
Villages N = 33											
Original	90	53.4	0.161	25.2	0.287	64	25.2	0.271	45	25.0	0.287
Repeat	64	49.9	0.168	32.6	0.233	40	28.1	0.249	24	27.0	0.244
Difference		-3.5	0.007	+7.4	-0.054		+2.9	-0.022		+2.0	-0.043

Table 3

Direction of change in morph-frequencies in the three study areas. Figures with an asterisk are formally significant ($p < 0.05$), ignoring those showing no change, the great majority of which represent 100% or 0% of the morph concerned

Site/Feature	Increase	No change	Decrease	Max decrease	Max increase	Changes of 20% or more
Sheffield						
Yellow	43*	1	22*	-40.1	43.4	16
Unbanded	14*	23	29*	-27.3	51.3	7
Midbanded	23	12	31	-45.1	69.7	6
Punctate	29	7	30	-31.8	58.4	12
Wrocław						
Yellow	12	0	7	-25.4	27.7	4
Unbanded	7	0	12	-31.7	29.1	2
Midbanded	11	0	8	-36.6	29.2	4
Trifasciate	8	1	10	-47.2	25.1	2
Villages						
Yellow	20	0	14	-40.0	31.1	7
Unbanded	11*	0	23*	-45.8	68.4	7
Midbanded	13	1	20	-38.0	29.2	7
Trifasciate	14	6	14	-37.5	39.9	6

slight, if consistent, decline in the frequency of yellow and increase in unbanded shells appears fortuitous. When direction of change, rather than magnitude is considered, however (Table 3), there are similar trends in all three regions. The significant results for Sheffield may simply reflect the larger number of samples involved. In Sheffield, a consideration of habitat, and of habitat change (Table 4), reinforces the suspicion that there has been systemic change in the frequency of yellow shells, partly associated with increased shade. No other morph shows such consistency. We use the word "suspicion" in recognition that an analysis of paired (nearest neighbour) samples from woods and more open sites in the earlier survey failed to show significant differences (Cameron *et al*. 2009).

Table 4

Changes in the mean frequency (%) of yellow shells in Sheffield in relation to the habitat stability or change

Sheffield	2007	2023	Difference	N
Wood-wood	37.3	32.3	-5.0	7
Scrub-wood	73.8	64.8	-9.0	8
Scrub-scrub	54.2	49.5	-4.7	14
Intermediate to scrub+wood	58.8	54.5	-4.3	7
Intermediate-intermediate	54.1	50.0	-4.1	26
Open-open	60.0	57.4	-2.6	4

Regardless of any systemic change, there are many cases of large changes in morph-frequencies, some of more than 40%. They are not consistent in direction (Table 5). With sample sizes usually greater than 50, changes of 20% or more are likely to be formally significant, but with a large number of sites, about 5% would be expected to show a false positive if no change had occurred. Since *c*. 16% pass this threshold, and some by much more than 20%, it is clear that some changes are real. They are not associated with habitat change. There is no evident difference among the regions.

Discussion

Our results demonstrate clearly the impermanence of urban habitats (Gilbert 1989). While there are relatively stable habitats, such as allotment gardens, churchyards and cemeteries, most populations are found in derelict or undeveloped sites, often isolated

Table 5

Aggregate changes in all four morphs in each area by percentage change, regardless of the direction. Given sample sizes of c. 50 or more, most changes of more than 20% will be formally significant. The percentage of such samples is given in bold. The range of change goes to extremes in both directions

Change	Sheffield	Wrocław	Villages
< 10%	173	44	70
10-19%	48	20	37
20-29%	25	9	14
30-39%	9	2	8
40%+	9	1	3
% > 20%	**16.3**	**15.7**	**19.0**
Range			
Yellow	-40.1 to 43.4	- 25.4 to 27.7	-40.0 to 31.1
Unbanded	-27.3 to 51.3	-31.7 to 29.1	-45.8 to 68.4
Mid-banded	-45.1 to 69.7	-36.6 to 29.2	-38.0 to 29.2
Punctate/Trifasciate	-31.8 to 58.4	-47.2 to 25.1	-37.5 to 39.9

by areas of development or intensive management. Even in apparently stable habitats, changes in management practice, including the use of herbicides, may render sites temporarily unsuitable.

At the time of the original surveys (Cameron *et al.* 2009), Wrocław had large areas of undeveloped land; these are now becoming fewer as development has been rapid. In Sheffield, development has been slower, but suitable habitats, often on derelict industrial sites, were more isolated initially. In many cases derelict sites have become more densely shaded, and others have been cleared.

We cannot account for the decline in both occurrence and apparent density of *C. nemoralis* in both cities and the region around Wrocław in the period between the two surveys. Although anecdotal evidence given by many people to R.A.D.C. suggests that, at least in the UK, it is not a range-wide phenomenon, in Poland the decline appears to be widespread. The reasons likely include habitat loss, also in the form of manicure-style management of public green spaces, as well as increased and often massive usage of molluscicides to fight invasive slug species. Similar declines in occurrence in intensely managed areas in western Europe have been observed already over a decade ago (Ożgo 2012).

While we cannot tell if previously unoccupied sites are now colonised, the apparent decline, most especially in occurrence, indicates that spread and genetic exchange between populations is likely to be severely limited. There is no significant decline in our estimates of F_{st} that might indicate genetic exchange among populations. The overall pattern of stasis, sometimes with small selective changes in morph-frequencies, is one found in many other studies, usually with longer periods of time between surveys than here (e.g. Wolda 1969; Cowie & Jones 1998; Ożgo & Schilthuizen 2011; Silvertown *et al.* 2011; Cameron & Cook 2013). We have tenuous evidence for a systemic decrease in yellow shells, and an even weaker trend for an increase in unbanded shells. We cannot point to a likely cause, since what evidence we have over the range as a whole, as in some of the references above, suggests an increase in yellow shells related to climate change.

While a longer interval between surveys might strengthen these trends, we note a number of substantial changes in morph-frequencies, sometimes exceeding 40%, that may go in opposite directions, partly accounting for the overall pattern of stasis. It seems unlikely, given estimates of selection in other studies, that these are the product of strong selection acting in opposite directions within a small area not subject to any evident local, but different, environmental changes. Given the decline in abundance recorded in all the regions studied here, it seems more likely that bottlenecks have altered the composition of populations, or that local extinction has been followed by recolonisation from elsewhere.

The difficulty of linking changes in such recent and relatively isolated populations to any cause can be illustrated by comparison with another resurvey in an area of stable habitat with continuous and abundant populations of *C. nemoralis* in Derbyshire, UK (Cameron *et al.* 2013). Here (Table 6), a systemic decline in yellow shells was precisely coincident with a habitat change from grassland to scrub, while in another study (Cameron & Pannett 1985), historical evidence on the age of woodland showed that morph-frequencies in woods less than 100 years old had not fully adjusted to expected values found in ancient woodland. In contrast, studies of urban populations, unstable and impermanent, highlight the underestimated aspects of evolutionary processes: bottlenecks, founder effects and local extinction and recolonisation.

Table 6

Changes in the frequency of yellow shells (%) in the three study areas and in Deepdale (Derbyshire, UK, see the text) over a 43 year timespan. Eleven contiguous sites in Deepdale had turned from grassland to scrub. All showed a reduction in the number of yellow shells, running counter to the non-significant trend in the remainder. The small (often zero) numbers of banded shells in many samples makes the analysis of other morphs unreliable. Data from Cameron *et al.* (2013)

Change	Wrocław	Villages	Shefield	Deepdale total	Deepdale scrub	Deepdale ex scrub
N	19	33	66	58	11	47
<10%	57.9	51.5	53.0	72.4	36.4	80.9
10-20%	21.1	30.3	19.7	24.1	54.5	17.0
20-30%	21.1	9.1	16.7	3.4	9.1	2.1
30%+	0.0	9.1	10.6	0.0	0.0	0.0

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Author Contributions

Research concept and design: M.O., R.A.D.C., E.K.-K.; Collection and/or assembly of data: M.O., R.A.D.C., E.K.-K.; Data analysis and interpretation: M.O., R.A.D.C., E.K.-K.; Writing the article: M.O., R.A.D.C., E.K.-K.; Critical revision of the article: M.O., R.A.D.C., E.K.-K.; Final approval of article: M.O., R.A.D.C., E.K.-K.

Conflict of Interest

The authors declare no conflict of interest.

Supplementary Materials

Supplementary Materials to this article can be found online at:
http://www.isez.pan.krakow.pl/en/folia-biologica.html

Supplementary files:

SM.01. Location, habitat type and composition of original and re-survey samples in Sheffield.

SM.02. Location, habitat type and composition of original and re-survey samples in Wrocław.

SM.03. Location, habitat type and composition of original and re-survey samples in settlements surrounding Wrocław.

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