

Table 3. Mean values of ingestion rates, growth rates and conversion indexes. WIR: Wet Ingestion Rate (mg of wet matter d<sup>-1</sup> animal<sup>-1</sup>); IR: Dry Ingestion Rate (mg of d.m. d<sup>-1</sup> animal<sup>-1</sup>); GR: Growth Rate (mg mg<sup>-1</sup> d<sup>-1</sup>); CI: Conversion Index = WIR / live wt growth rate); OIR / ΔSBOM = Organic Ingestion Rate (mg d<sup>-1</sup> animal<sup>-1</sup>) / Organic Soft Body Increase (mg d<sup>-1</sup> animal<sup>-1</sup>); MIR / ΔASW = Mineral Ingestion Rate (mg d<sup>-1</sup> animal<sup>-1</sup>) / Inorganic Shell Wt Increase (mg d<sup>-1</sup> animal<sup>-1</sup>)

	WIR	IR	GR	CI	IR / ΔTDW	OIR / ΔSBOW	MIR / ΔASW
L	871.9 ± 139.4	50.6 ± 8.1	0.019 ± 0.010	14.46 ± 6.03	5.86 ± 2.39	11.83 ± 4.83	1.99 ± 0.82
Wh	211.4 ± 55.7	64.5 ± 17.0	0.060 ± 0.021	0.88 ± 0.42	2.07 ± 0.98	3.21 ± 1.52	1.49 ± 0.71
Wl <sub>a</sub>	191.4 ± 63.2	183.0 ± 60.5	0.108 ± 0.023	0.36 ± 0.11	2.98 ± 0.93	4.85 ± 1.52	1.94 ± 0.61
Wl <sub>b</sub>	100.8 ± 28.3	93.5 ± 26.3	0.090 ± 0.024	0.26 ± 0.11	3.04 ± 1.00	3.29 ± 1.21	3.69 ± 1.82
G	88.0 ± 18.5	84.0 ± 17.6	0.036 ± 0.009	0.79 ± 0.32	3.94 ± 1.14	4.83 ± 1.41	1.45 ± 0.42

Growth rates computed from live-weight increases for G and high M.C. diets agree with previous results for artificial meals (Daguzan, 1985, Fonollá *et al.*, 1980), Wl diets showing higher rates. Significant differences arise among food conversion factors (ANOVA for CI: F=46.1  $P < 0.0001$ ) being largest for lettuce, values of  $0.8345 \pm 0.3715$  and  $0.3105 \pm 0.108$  appearing for Wh and G and both Wl diets respectively. Conversion factors lower than unity on a food wt/ snail live weight basis have been reported by Jess & Marks (1995) and probably result from a more precise determination of "true" ingestion, as opposed to offered ration. In fact, when gross growth efficiencies are calculated (IR / ΔTDW, OIR / ΔSBOW, MIR / ΔASW), similar factors of 3.62 for organics and 1.83 for minerals appear for every diet, with the exceptions of lettuce and G for organics and inorganics respectively.

Table 4. Mean values of parameters of energy balance. OIR = Organic Ingestion rate (mg d<sup>-1</sup> animal<sup>-1</sup>); AE = Assimilation Efficiency (%); VO<sub>2</sub> = Oxygen Consumption (ml O<sub>2</sub> d<sup>-1</sup> animal<sup>-1</sup>); SFG = Scope For Growth (J d<sup>-1</sup> animal<sup>-1</sup>). Oxycaloric Coefficient: 20 J/ml O<sub>2</sub>. S.D.= Standard deviation

	OIR	AE	VO <sub>2</sub>	SFG
Lettuce	41.82 ± 6.69	82.54 ± 2.98	6.65 ± 3.59	564.3 ± 116.2
Water High	40.95 ± 10.78	82.66 ± 5.20	8.67 ± 4.23	563.3 ± 152.5
Water Low <sub>a</sub>	122.24 ± 40.39	61.91 ± 5.88	12.91 ± 4.22	1362.9 ± 528.7
Water Low <sub>b</sub>	61.98 ± 17.42	55.92 ± 11.39	9.71 ± 3.09	518.6 ± 320.5
Chicken	69.64 ± 14.62	53.64 ± 17.43	7.46 ± 3.18	502.4 ± 131.7

Results from SFG determinations have been summarized in Table 4. Differences in assimilation efficiency are significant (ANOVA F= 20.23  $P < 0.0001$ ) with two values for high and low M.C. meals respectively:  $82.6\% \pm 4.13$  cf  $57.38\% \pm 12.4$ . Figures for water-enriched foods relate well to data reported for lettuce and cabbage (Charrier & Daguzan, 1980; Charrier, 1980) and results for dry foods agree with digestibility coefficients given by Fonollá *et al.*, (1980). Such variation is associated with the negative effect of higher rates of food intake (as is the case in dry-matter terms for low moisture-content diets) upon efficiency of organic

absorption, although it does not explain the similarity of AE (%) within this group, where large differences in food intake are evident. This aspect will be discussed later.

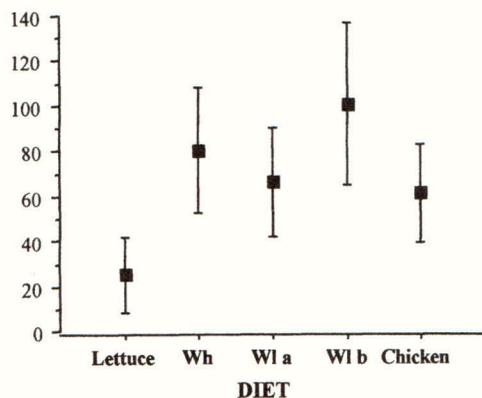


Figure 1. Gravimetric vs. scope for growth (SFG) determinations of growth rate. Values are means of Organic weight increase / Accumulated SFG in percentage units, showing bars for confidence limits : CL<sub>95</sub>.

A mean SFG of  $538.56 \text{ J d}^{-1} \text{ snail}^{-1} \pm 188.85$  was found for every meal except WI<sub>a</sub>, which showed increased values ( $1362.92 \pm 528.71$ ). Growth rate in organics obtained from exponential equations accounts for 75.6% ( $\pm 35.1$ ) of SFG recordings, lettuce exhibiting reduced recovery (Figure 1). Such differences could well be explained by variability of investments in mucus production. Although strict comparisons are not possible, available data for molluscs indicate that energy expended on mucus secretion may represent between 12 and 40% of energy intake (Horn, 1986; Peck, *et al.*, 1993).

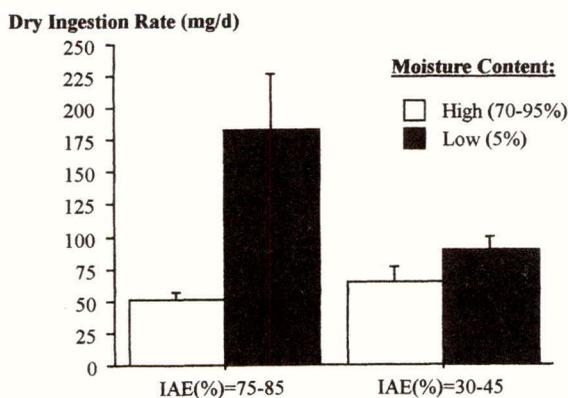


Figure 2. Ingestion rate of d.m. ( $\text{IR} = \text{mg d}^{-1} \text{ animal}^{-1}$ ) vs. M.C. of foodstuffs and absorption efficiency of mineral compounds of diets (IAE%).

As a conclusion, differences in ingestion rate in dry-matter terms explain 80% of the variation found in SFG and thus in growth rate. Consequently, differences of food intake within similar moisture-content meals require some explanation. If data for wet ingestion rate for lettuce are somehow related to gut capacity on a volume basis, the low figures found for WI would imply

unexplained constraints to ingestion rate in terms of organic absorption requirements (a mean 82% AE). Similarly, dry matter processing for G and W<sub>1b</sub> comprised half the amount eaten by snails from W<sub>1a</sub> food, all meals showing 57% of AE. As shown in Figure 2, where two-factor ANOVA results were highly significant for both terms and interaction, in both sets of comparisons, absorption efficiency for minerals was significantly low. Since the body composition of snails indicates that dry matter is equally distributed among organic and inorganic materials, it is tempting to suggest that under active development, coordinated growth would imply that constraints set to absorption impose longer retention times and, consequently, reduced ingestion rates.

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### Dissecting size-frequency data relating to terrestrial snails

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#### ABSTRACT

Size-frequency histograms are often used as a method of presenting observations of continuous variables which have been sampled discontinuously. For example, regular measurements of size are used to illustrate demographic changes. Growth rate in the field is sometimes inferred from such histograms. However, by considering results from a population of the terrestrial snail *Monarch cantiana*, it appears that size is not necessarily an indicator of age. This conclusion was reached by colour coding individual snails and then monitoring them for twelve months on arable land in South East England. These results have implications for many situations where intermittent sampling of snails leads to conclusions about cohort growth and recruitment of snails.

#### INTRODUCTION

During surveys of terrestrial snails on arable farmland in the Debden Valley in South East England in August 1997, 71% of a population of live *Monarcha cantiana* (Montagu) were found to be fully-grown, and there was an unusual lack of small snails. *M. cantiana* can grow by 2mm in 3 weeks in the laboratory and can have fully developed reproductive system at approximately two thirds full size (Chatfield, 1968); they can also lay 90 eggs in one batch (Taylor, 1917). It thus appeared that low fecundity was unlikely to be the reason for the low proportion of young snails in this Debden population. Alternatively, larger snails may have colonised from adjacent ditch habitats and biased the size distribution towards larger snails. Field and laboratory experiments were therefore designed to test whether colonisation was an important factor for this population of *M. cantiana*. It was also intended to test some of the anecdotal yet much quoted observations from the classic study on terrestrial snail ecology by Boycott (1934).

#### METHOD

A 9.02 m<sup>2</sup> grassland plot (O.S. map ref. TL 552 342) was cleared with an Allen sythe and seeded with mixed vegetation including carrot, turnip, cabbage and Jerusalem artichoke. Other plants grew in the sample plot during the investigation, including grasses, *Urtica dioica*, *Cirsium arvense* and *Papaver somniferum*. The plot was 4.3 metres from a ditch field-margin. We measured the average distance moved by *M. cantiana* in a field situation as 37.5 cm in 24 hours, so the plot of mixed vegetation was easily accessible from the ditch field-margin within 12 days.

In October 1997, the mixed vegetation area was searched by hand for four hours and 30 adult, but no juvenile, *M. cantiana* were found. The shells of these 30 individuals were numbered and the snails released where they had been found. The site was monitored for a year during which time, as before, the surrounding grass was cut in August with an Allen scythe. The vegetation on

the mixed vegetation plot was left undisturbed between monitoring sessions. From October 1997 to September 1998, *M. cantiana* were collected by hand each month from the mixed vegetation plot, which now included relatively tall vegetation such as grasses and *Urtica dioica*, both of which are known to be a food resource for *M. cantiana*. The surrounding 7.4 m<sup>2</sup> of grassland was also searched. In the first survey, all *M. cantiana* were individually weighed and marked. In subsequent monthly surveys, unmarked individuals were marked using a different colour for each month. In September 1998 the ditch field-margin was searched to see if snails marked in the area of mixed vegetation had moved as far as the ditch field-margin.

For snails up to 10mm in size, there was a close correlation between shell breadth and mass ( $r_s=0.943$   $n=138$   $P < 0.02$ ). For larger snails, the correlation was less strong, presumably due to reproductive activity causing variations in the weights of adults ( $r_s=0.898$   $n=117$   $P < 0.02$ ). On the basis of this high correlation, the size of juvenile snails could be obtained by weighing them in batches. Such snails were marked and released on the same day as capture.

## RESULTS AND DISCUSSION

In August 1998, considerably more *M. cantiana* were found amongst taller mixed vegetation (61.3/m<sup>2</sup>, of which 22.7/m<sup>2</sup> adults) than in (i) grassland without the taller herbs (between <1 and 4 /m<sup>2</sup>) (ii) an adjacent field-margin (between 18 and 44 /m<sup>2</sup>). Thus, as Boycott (1934) observed, the type of vegetation influences snail abundance. However, contrary to Boycott's observation in 1934 that "we seldom see young snails much more abundant than the adults will be later on, and the main loss falls I believe on the eggs and the infant young" 959 juveniles and 242 adults were recorded within the sampling area in May 1998 followed by 634 juveniles and 373 adults in August. Thus, in this newly colonised site, small (juvenile?) *M. cantiana* were much more abundant than were the adults later on. These results suggested that growth of juvenile *M. cantiana* was slower than indicated in the literature (Chatfield, 1968). Growth rate was therefore investigated both in the laboratory and in the field. For one year, *M. cantiana* were sampled monthly, weighed, marked and released on the mixed-vegetation site. The weight gave an indication of snail size and, over time, the mark-colour gave a minimum age, to the nearest month, for an individual snail. For example, a July 1998 sample from the mixed vegetation site contained 269 marked *M. cantiana*. Of these, 122 had been collected and marked in surveys between December 1997 and April 1998. These 122 individuals therefore had a minimum age of between 3 and 7 months.

Chatfield (1968) observed that *M. cantiana* hatchlings were approximately 1.6mm in size. Thus the aforementioned 122 *M. cantiana* (aged at least 3-7 months) might be expected to be adults with a shell diameter of 9.6 to 20 mm. These 122 individuals were weighed. From a regression based on the previous weight/shell breadth relationship, their inferred shell breadth ranged from 3 to 17 mm, and 63% were small enough to be juveniles (< 10mm shell diameter). One individual captured, marked and released on 17 March 1998 had a shell breadth of 3 mm when it was recaptured three months later on 7 July 1998. Thus a snail, which on the basis of its small size appeared to be a hatchling, might in fact be four months old.

This apparent slow growth of *M. cantiana* was then investigated in the laboratory. A turf containing *M. cantiana* eggs was collected in August 1998 and monitored for eleven months until March 1999. The turf, in a plastic container with nylon netting over the top, was placed in the vicinity of the field-margin site. Figure 1 shows the increase in weight of juvenile *M. cantiana* from 24 weighing sessions of snails in this container over a 7 month period. There was

15% mortality in the first two weeks and 44% were alive by 25/03/1999. Figure 1 also shows that growth in any cohort was slow and uneven, with the range in size increasing with time and few snails reaching reproductive size by March 1999. For example, of 27 juveniles (23 eggs and 4 hatchlings) weighing between 0.005 g and 0.015 g on 12/08/1998, only 12 were alive by 25/03/1999. These 12 survivors ranged in weight from 0.015 g to 0.260 g. The smallest at 0.015 g was still the weight of a hatchling. Only four of the survivors reached adulthood at between 0.2 g and 0.3 g.

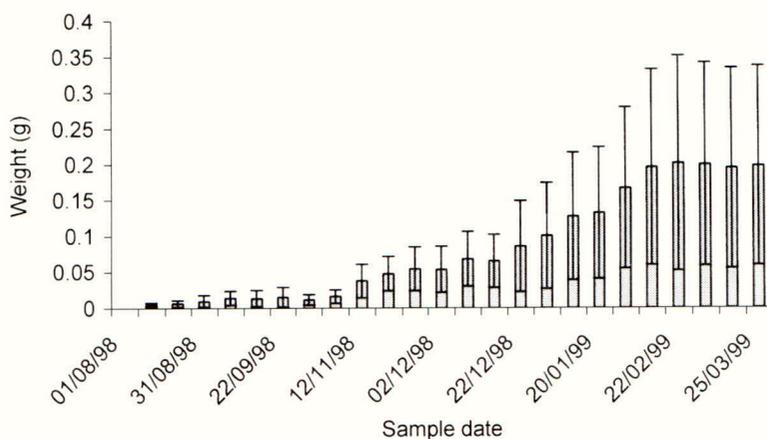


Figure 1. Increase in weight of a cohort of juvenile *Monarcha cantiana* in the laboratory (mean +/- SD)

Thus, death of an apparently juvenile snail weighing < 0.2 g might in fact be the death of a snail seven months old. Similar growth variation has been noted for *Oxychilus* sp. in the laboratory (Regina Cunha *pers. comm.*) where consistent growth of snails within a cohort was achieved only when eggs were hatched and young reared in sterile conditions. Parasites and pathogens may therefore be a cause of the slow growth described above.

This possibility of slow growth is important, given the standard practice of seasonal collection and counting of snails, where results are presented as histograms (eg. Baker, 1968 for *Helicella caperata* Mont., Baker, 1969 for *Cochlicopa lubrica* (Müller), Chatfield, 1968 for *M. cantiana*; Staikou, 1998 for *Cepaea vindobonensis*). The limitations of this method of presentation may be seen by reference to Figure 2 and Figure 3.

In Figure 2, adult *M. cantiana*, present in November and December, appear to die during the winter. Only juveniles from autumn reproduction activity appear to be present from January to April. Juveniles then appear to grow to reproductive age by July 1998. This is in line with expectations from similar histograms in the literature (Chatfield, 1968).

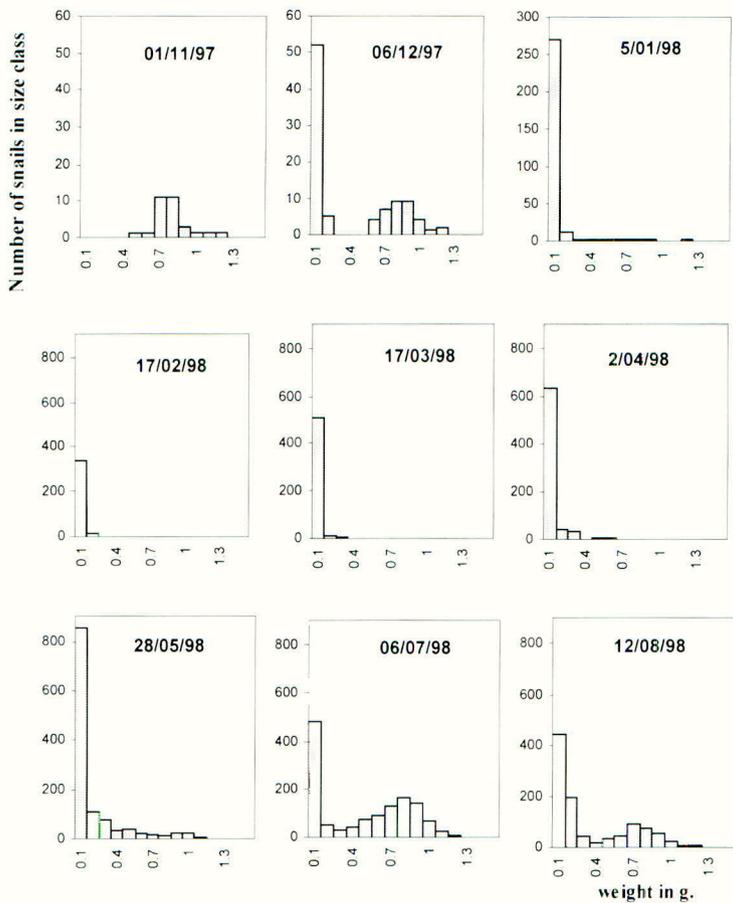


Figure 2. Histograms of *Monarcha cantiana* abundance by weight, sampled from the mixed vegetation site between 1/11/1997 to 12/08/1998.

Whilst the presentation of results in Figure 2 is qualitatively correct for abundance, the following analysis, equivalent to a dissection of the data, shows that quantitative monitoring gives a better resolution. By July 1998, there was a bimodal frequency histogram of snail weight of *M. cantiana* at the newly colonised site on the mixed-vegetation plot. However, this was not just due to the offspring within a new colony reaching reproductive age. As may be seen from Figure 3, many snails marked between November 1997 and April 1998 were still of small juvenile size ( $<0.1\text{g}$ ) by July 1998 and there was an influx of unmarked adult snails, suggesting re-colonisation of the site. The increase in juveniles and the influx of unmarked adult snails was so large in May and July that the abundance data had to be  $\log_{10}$  transformed (Figure 3).

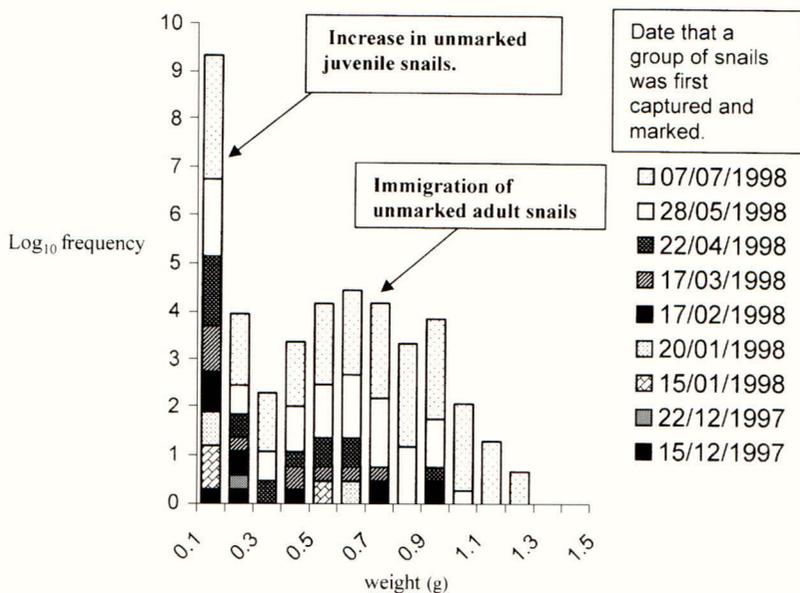


Figure 3 Frequency histogram of *Monarcha cantiana* abundance in July 1998 at a mixed vegetation site showing the increase in juveniles and immigration of adults.

Similarly, when using a finer scale for the abundance of juvenile *M. cantiana* up to 0.1 g, there was no big influx of hatchlings in December 1997 but rather small numbers of snails in the different size categories (Fig. 4). By September 1998, a large population of snails was observed in the ditch 4.3 metres away from the mixed vegetation site. Few snails were observed in the grass further into the field. The ditch margin was hand searched for macro-snails for a period of four hours. 19% of the 548 *M. cantiana* found on the ditch field-margin were already marked, indicating that they had been first captured in the mixed vegetation site 4.3 metres away. Some were adults that had been captured and released in the tall vegetation in June and July. Thus there may be a single population of snails which occupies the whole of the 40 m<sup>2</sup> site.

Thus, it appears that field margins, especially if they comprise ditches, can act as reservoirs of snail populations and *M. cantiana* can migrate out of such a refuge and colonise adjacent farmland. Here, *M. cantiana* expanded its range and occupied a habitat which then provided less than ideal conditions for growth, with the result that few snails reached reproductive age. However, this was not just due to mortality, since many juveniles survived for at least six months yet failed to grow and mature.

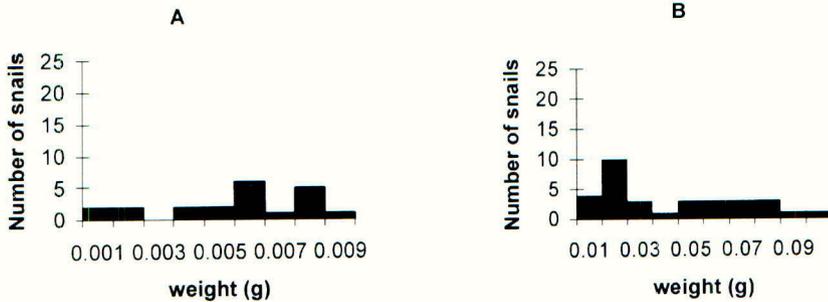


Figure 4 Frequency histograms of juvenile *Monarcha cantiana* 6/12/1997.  
(A) 0.001 g to 0.01 g (B) 0.01 g to 0.1 g

These results also show that the size-frequency histograms can mask features such as juvenile growth retardation. It may therefore be necessary to carry out detailed growth experiments to fully appreciate the population dynamics. In this example of *M. cantiana*, immigration from the ditch field-margins biased the size-frequency distribution and masked retardation of growth in juvenile snails. This developmental retardation may have had pathogenic or parasitological causes. These results, obtained by dissecting the size-frequency data, may have implications for many situations where intermittent sampling of snails leads to conclusions about cohort growth and recruitment.

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**Persistence and shell band morph frequencies in urban populations of *Cepaea***

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**ABSTRACT**

In Prague, *Cepaea hortensis* is an autochthonous species while *C. nemoralis* was introduced artificially. Local populations of both species were surveyed in 1994-2003. In *C. hortensis*, abundances at particular sites varied between years and several local populations became extinct. Shell band and colour morph frequencies differed between sites but at each site persisted in time. *C. nemoralis* was released at nine sites in 1995. Introduced populations became established at four sites and spread to one new site. Colonization succeeded regardless of previous occupation of sites by *C. hortensis*. At some sites, frequencies of shell-band morphs after introduction remained similar to founder samples, whereas at other sites they changed.

**INTRODUCTION**

In the Czech Republic, populations of *Cepaea hortensis* Müller are widespread, in rural, urban and ruderal situations covered by different vegetation. Sites include dry and humid meadows, hedgerows, shrubs and gardens (Honek, 1995). By contrast, *Cepaea nemoralis* (L.) populates the north-western part of the territory from where it spread south-eastwards and lives only on sites affected by human activity, frequently comprising cemeteries and railway stations. Prague is situated outside the area where *C. nemoralis* is common and there are only a few naturally established populations (Jurickova, 1995), always at small isolated sites. This situation offered the possibility of studying experimental introduction of *C. nemoralis* populations into a new, apparently convenient but still unoccupied, territory. This colonisation experiment was performed in 1995 when *C. nemoralis* was released at several sites at Praha-Ruzyne. The survival, abundance and shell colour and band morph frequency of introduced *C. nemoralis* populations, as well as indigenous *C. hortensis* populations were then observed every year. In this case study, we report on the changes of abundance and phenotypic composition of both species.

**MATERIAL AND METHODS**

The study was made at twenty sites situated in the North-West suburbs of Prague (between 50°04'35"-50°05'11" N and 14°18'14"-14°19'37" E) (Figure 1), in 1994-2003.

*C. hortensis* populations were surveyed at eleven sites where the counts were continued for more than four years. Eight sites lay close together and the minimum distance between sites was 50 m. These near sites were separated by roads, fences, hedgerows or other barriers that made movement of animals difficult but did not prevent exchange of individuals between populations. The populations were surveyed once each year, on a rainy day in May or June. At each site snails were collected for approximately ten minutes and living adults and large

juveniles were then counted. Shell band morphs were registered into three classes (0-0-0-0-0, 1-2-3-4-5, animals with any confluent bands), shell colour was classified as yellow or pink. The standardised sampling effort enabled comparisons of snail abundances between years. Because vegetation and ground surface quality differed between sites, the data reveal annual changes within a site but cannot be used for comparison between sites.

*C. nemoralis* were introduced in 1995 from a sample of 391 adult and large juvenile animals collected from a natural population at Zalhostice (50°32'N, 14°06'E) (Table 1, source population). The snails were sorted by shell band and colour morph, divided into groups of 7 - 50 individuals of identical morph, and released on nine sites which appeared suitable for their survival, on May 14 - 17. The sites were then regularly visited from 1997. The visits were made on rainy days in May or June and lasted up to forty minutes to ensure that no animals were overlooked. Shell band morphs were classified as 0-0-0-0-0, 0-0-3-0-0, 0-0-3-4-5, 1-2-3-4-5 (a few animals with confluent bands were classified as respective band morphs), shell colour as yellow or pink. An indigenous population of *C. nemoralis* (15) was surveyed from 1999. It was approximately 150 m away from Site 14, where an introduced population had been released in 1995, but the two sites were separated by a creek, so migration between them was improbable.

The number of animals collected in ten minutes (abundance) were converted into  $\log_{10}(n+1)$  and mean between-year changes of abundance were calculated (Williamson, 1972). To compare the differences in proportions of colour morphs between populations of *C. hortensis*, the data for particular years were arcsin transformed and averaged over the total period of observation.

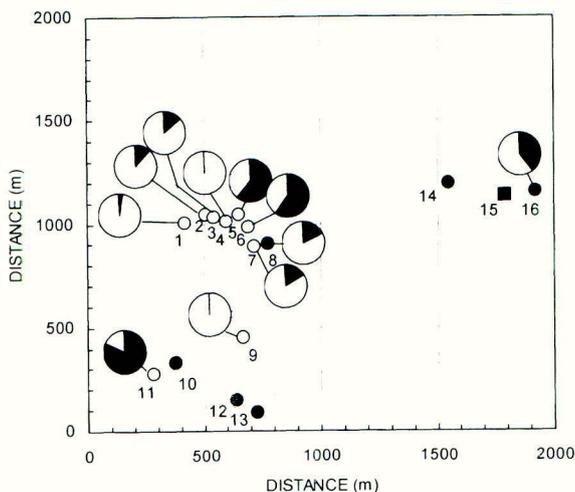


Figure 1. Relative position of Sites 1 - 16 (Sites 17-20 outside the area) and proportion of unbanded morph (black) in pooled samples over all years of *C. hortensis* populations. Solid symbols: Sites of introduced (circles) and indigenous (square) *C. nemoralis* populations.

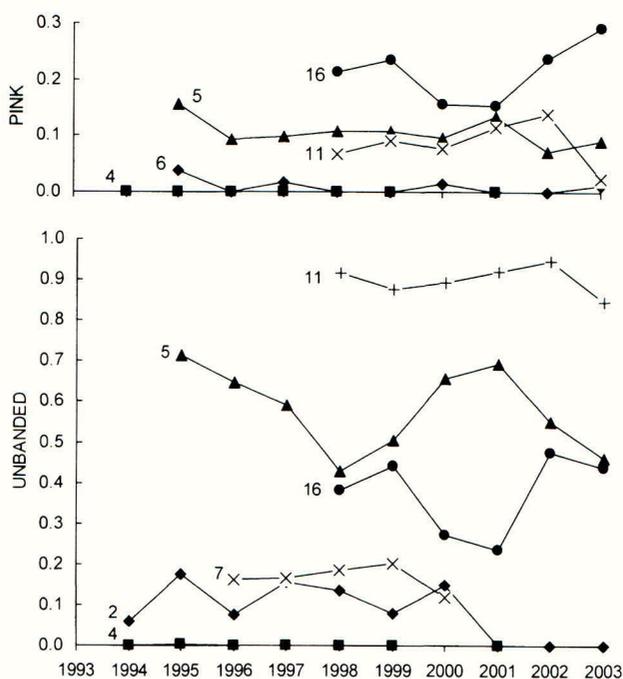


Figure 2. The proportion of pink morph (above) and unbanded morph (below) in some populations of *C. hortensis*, 1994-2003. Site numbers as in Figure 1.

## RESULTS

### *C. hortensis*

Populations of *C. hortensis* were surveyed at eleven sites starting between 1994 and 1998. During this period, populations became extinct at four sites. At Site 4, extinction could be attributed to planting of ornamental shrubs. The population at Site 9 disappeared without any visible change of habitat (dry uncut meadow). Two populations (7 and 8) disappeared following construction work. Another two populations (2 and 3) disappeared temporarily, without a visible change of site quality, but the sites were recolonised 1 or 2 years later. Average year-to-year change of abundance at these sites was  $0.613 \pm 0.071$  log units. Changes of abundance in populations 1, 5, 6, 11 and 16 were smaller, comprising  $0.294 \pm 0.043$  log units. Thus many local populations in this suburban environment were subject to large variation in numbers. The population of Site 1 appeared after 1998, probably by colonisation from Site 2.

The frequency of shell band (Figure 1) and shell colour morphs varied between localities. The differences in proportion of unbanded morphs were significant, even between sites which were close together e.g. 1 and 3 (130 m distance, 2.9 and 14.6 percent unbanded,  $P < 0.05$ ) or 3 and 4 (60 m distance, 14.6 and 0.2 percent unbanded,  $P < 0.01$ ). The differences persisted for several years even when the sites were not separated by physical barriers and the exchange of

individuals between populations was possible. Similar differences were found for the proportion of pink coloured morphs, e.g. between sites 5 and 6 (70 m distance, 1.5 and 10.6 percent pink,  $P < 0.01$ ). The frequencies of morphs at particular sites were stable over the years (Fig. 2).

Table 1. Introduced and indigenous populations of *C. nemoralis* at Praha-Ruzyne. Site numbers (No.) as in Fig. 1. Source sample: Morph - composition of introduced samples, N - number of individuals, Spec - species present at the site before colonization (Ch - *C. hortensis*, Hp - *Helix pomatia*). Established population: Pooled number of individuals of particular shell banding morphs and colour morphs (Y -yellow, P - pink) sampled in 1997-2003 in populations established at Prague (no data - population did not survive). Site 13 was discovered only in 2002

No.	Source sample		Established population						
	Morph	N	Spec.	0-0-0-0-0	0-0-3-0-0	0-0-3-4-5	1-2-3-4-5	Y	P
Introduced populations									
8	P, 0-0-3-0-0	28	Ch, Hp	0	30	0	4	5	29
10	Y, 0-0-3-0-0	50	Ch, Hp	0	65	9	2	72	4
12	P, 0-0-0-0-0	41	Ch, Hp	28	213	9	20	209	61
13			Ch	0	72	11	1	84	0
14	Y, 1-2-3-4-5	49	Ch, Hp	--	--	--	--	--	--
16	P, 1-2-3-0-0	7	Ch	7	21	8	6	26	16
17	P, 1-2-3-4-5	50	Ch	--	--	--	--	--	--
18	P, 1-2-3-0-0	28		--	--	--	--	--	--
19	Y, 0-0-3-0-0	14		--	--	--	--	--	--
20	P, 0-0-3-0-0	48	Ch, Hp	--	--	--	--	--	--
Indigenous population									
15			Ch	357	0	0	154	93	418

Table 2. The proportion of *C. nemoralis* shell band morphs in the sample of source population (Zalhostice) and pooled sample of populations established at Prague

	N	Band morph				Total
		0-0-0-0-0	0-0-3-0-0	0-0-3-4-5	1-2-3-4-5	
Source population (Zalhostice 1995)						
Yellow		0.0	16.4	0.0	12.5	28.9
Pink		16.9	19.4	9.0	25.8	71.1
Total	391	16.9	35.8	9.0	38.4	
Introduced populations (Praha, all Sites 1997-2003)						
Yellow		0.0	65.8	6.9	5.5	78.3
Pink		6.9	13.4	0.4	1.0	21.7
Total	506	6.9	79.2	7.3	6.5	

### *C. nemoralis*

The persistence of nine populations released in 1995 was followed (Table 1). In 1997, juveniles were found at four sites (8,10,12,16) where the abundance further increased during the following years. At one site (17) only two adults were found in 1997 and one in 1998, probably those released in 1995, and the population became extinct four years after release. No snails were found at four sites (14, 18, 19, 20) where the introduced populations apparently became extinct within two years from release. The success in establishing a new population was not correlated with shell band or colour morph, percentage of juveniles, or size of the released sample (Table 1). Previous occupation of the site by *C. hortensis* or *Helix pomatia* did not influence the colonisation success (Table 1). A population at Site 13, 70 m from Site 12 was discovered in 2002 (Figure 1). The population of Site 13 may have been founded by emigrants from population 12, as morph proportions on both sites were similar.

Shell band and colour morph proportions changed during the process of colonisation. The composition of the pooled sample of individuals found at the sites of release after introduction was significantly different from the composition of source population at Záhlostice (Table 2). The samples used to establish introduced populations were homogeneous in shell colour and band form. The populations at two sites (8, 10) largely maintained the frequency of morphs of the introduced sample while at two other sites (12, 16) the frequency of morphs differed from the original sample (Table 1). By contrast, the indigenous population discovered in 1999 maintained nearly constant morph proportion distinct from all introduced populations (69.9 per cent 0-0-0-0-0 pink, 11.9 per cent 1-2-3-4-5 pink, 18.2 per cent 1-2-3-4-5 yellow).

### DISCUSSION

This case study has indicated some causes of high colonisation and survival capacity of *Cepaea* species in man-affected environments. Populations of indigenous *C. hortensis* were subject to large variation in abundance and several local extinctions were caused by changes in vegetation, land use, and by construction work. However, some populations were able to recover and colonise new sites. Morph frequencies at particular sites were rather stable. Thus differences in percentage of colour or band morphs between sites persisted for years even in absence of isolation or apparent selection pressure. This persistence of differences in morph frequency was earlier observed in *C. nemoralis* (Wolda, 1959). The local variation in morph frequency was typical for urban *C. hortensis* populations while rural populations are often uniform even when they occupy large areas (Honek, 1995). The differences may be favoured by the mosaic character of urban environment as opposed to the uniformity of open landscape (e.g. steppe) habitats.

The capacity of *Cepaea* species to survive and adapt to new conditions was demonstrated also by the colonisation success of *C. nemoralis*. Nearly 50% of samples released in 1995 succeeded in establishing new breeding populations. This figure exceeds the average rate of colonisation success in animals estimated at 10% (Williamson, 1996).

The morph frequency in the pooled sample of *C. nemoralis* from Prague, born after colonisation, was significantly different from the source natural population. This may be attributed to fragmentation and segregation of phenotypes in the introduced samples and their different survival after release. However, recent studies have indicated the changes probably due to selection that exist even in natural populations persisting for a long time in an

undisturbed natural environment (Cowie and Jones, 1998). Selection thus might contribute even in our case. In fact, the source population of *Zalhostice* lived in a steppe locality (a steep south-oriented slope covered by grass) and may thus be exposed to a warmer and drier microclimate than the Prague populations.

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