Differential shell strength of *Cepaea nemoralis* colour morphs—implications for their anti-predator defence

Zuzanna M. Rosin · Jarosław Kobak · Andrzej Lesicki · Piotr Tryjanowski

Abstract One of the most spectacular evolutionary forces is predation, evidenced to stimulate polymorphism in many prey species. Shell colour polymorphism of the land snail *Cepaea nemoralis* is a well-known model in evolutionary research. Nevertheless, the knowledge on the ecological causes driving its evolution remains incomplete and proximal factors shaping predatory pressure on *C. nemoralis* morphs are unknown. We evaluated shell crushing resistance and thickness, constituting crucial snail anti-predator defences in two shell areas (the apex and labium) of eight *C. nemoralis* morphotypes differing in shell colour and banding pattern. A GLM showed a significant effect of shell colour, banding pattern and shell thickness on shell strength. Pink shells were stronger than yellow ones, and banded forms had stronger shells than unbanded snails. The labium (usually attacked by mice) was generally thicker and more resistant than the apex (usually crushed by birds). Thicker shells were more resistant to crushing, and the rate of shell strength increase per unit of shell thickness was greater in pink and banded individuals compared to yellow and unbanded ones. Yellow and unbanded morphs have been found to be preferred by mice in the previous studies, which suggests that shell strength may be an important trait used in prey selection by these shell-crushing predators. The differences in potential anti-predator defences among snail morphs, found in the present study, justify future research on direct effect of *C. nemoralis* morphs shell strength on predator selectivity.

Keywords Polymorphism · Shell crushing resistance · Labium · Banding type

Introduction

The importance of differential predation pressure has been well evidenced for the evolution and maintenance of polymorphism in many prey species, including mammals (Hoekstra et al. 2004), reptiles (Rosenblum et al. 2004), fish (Svänback and Eklöv 2011), insects (Ruxton et al. 2004; Rowland et al. 2008), crustaceans (Merilaita 2001; Hargeby et al. 2004) and gastropods (Johannesson and Ekendahl 2002). Therefore, morphologically variable species are excellent objects of studies on causes and effects of selective predatory pressure (Punzalan et al. 2005). Surprisingly, its role in the polymorphism of the well-studied the brown-lipped grove snail *Cepaea nemoralis* (L.) is still uncertain.

Populations of *C. nemoralis* exhibit genetic variability in shell colour (mainly yellow, pink or brown) and banding pattern (zero, one, three or five dark bands sometimes joined together) (Richards and Murray 1975). The knowledge on the ecological causes of maintenance of this polymorphic coloration is still incomplete despite over 100 years of studies (Cook 1998, 2005; Ożgo 2008; Cameron and Cook 2012; Pokryszko et al. 2012). Many factors may affect spatiotemporal variability in *Cepaea* shell colour, including genetic drift, migration, climatic selection, habitat heterogeneity and landscape structure (e.g. Jones 1974; Hutchison and Templeton 1999; Cameron and Pokryszko 2008; Le Mitouard et al. 2010; Silvertown et al. 2011; Ożgo 2012). Selective predation by birds has long been

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suggested as one of the main forces maintaining polymorphism in *Cepaea* shell coloration (e.g. Cain and Sheppard 1954; Allen 2004; Cook 2005; Punzalan et al. 2005; Rosin et al. 2011), but the exact mechanism behind this process remains uncertain.

Two main hypotheses have been formulated in attempts to explain differential predator selectivity toward *Cepaea* morphs, selection for crypsis (Cain and Sheppard 1950, 1954) and frequency-dependent selection (Clarke 1962). Cain and Sheppard (1950, 1954) showed that avian predation on yellow *Cepaea* was highest in the early spring and gradually decreased as the season advanced and vegetation developed. This pattern was explained by changes in habitat conspicuousness for the yellow morph (Cain and Sheppard 1950, 1954). On the other hand, Cook (1986) found no evidence that avian preference toward particular *Cepaea* morphs depended on background colour. Studies on the role of apostatic selection have provided evidence both in support of and against this hypothesis (Clarke 1962, 1969; Allen and Clarke 1968; Allen and Weale 2005). The latest study by Rosin et al. (2011) showed that mice prey most heavily on yellow unbanded and one-banded *C. nemoralis* morphs, whereas birds prefer colours other than brown.

In the field, *C. nemoralis* may be exposed to many predators, mainly birds, such as the blackbird *Turdus merula* L. and the song thrush *Turdus philomelos* C. L. Brehm, as well as mammals, such as mouse *Apodemus* sp., differing in their sensory capabilities, foraging behaviour and manner of prey handling (Morris 1954; Wolda 1963; Allen 2004). Thus, these predators may provoke different defence strategies. Crypsis, mucus production and the shell itself are the most important snail defences (Allen 2004). Whereas, the conspicuousness of *C. nemoralis* shell colouration for visual predators has been deeply studied (e.g. Sheppard 1951; Allen and Weale 2005; Surmacki et al. 2013), other features of its shell, such as thickness and strength, which are potentially important for predators are very poorly recognised (Jordaens et al. 2006). Moreover, there is some evidence that the dark pigmentation may strengthen the shell (Cook and Kenyon 1993). Therefore, it would be important to understand not only the effects of shell colour on crypsis but also on a direct resistance to predation.

According to optimal foraging theory, the shell thickness of optimum prey individuals should be small enough to allow their breaking, but at the same time the body size should be large enough to provide a worthwhile portion of food (Stephen and Krebs 1986; Quensen and Woodruff 1997; Norris and Johnstone 1998; Reed and Janzen 1999). Since some predators (e.g. mice) may operate by trial and error when searching for food (Rosin and Tryjanowski personal observations), it is possible that snails with more resistant shells show higher survival when exposed to predation, which has not been considered in studies on predation on *Cepaea* so far (e.g. Cain and Sheppard 1954; Clarke

1962). It has been shown that crushing predators impose a selective pressure on external skeletons of mussels (e.g. Durell et al. 1984; Krist 2002; Smallegange and van der Meer 2003), freshwater gastropods (e.g. Kitching and Lockwood 1974; Lewis and Magnuson 1999) and crustaceans (Huelsken 2011). However, only few papers have dealt with this problem in land snails (Gittenberger 1996; Quensen and Woodruff 1997; Moreno-Rueda 2009).

The aim of the present study was to evaluate shell crushing resistance among various *C. nemoralis* morphs. We hypothesised that shell resistance to breakage could be associated with its colour and banding type, as these features affect the susceptibility of snails to predators (e.g. Cain and Sheppard 1954; Rosin et al. 2011).

Material and methods

Study species

The genetic basis of the brown-lipped grove snail *Cepaea nemoralis* (L.) variability has been well investigated. Genes determining shell colour as well as band appearance and colour form a supergene. Genes determining shell and band colour are located close together. Brown colour is dominant over pink and yellow, whereas pink is dominant over yellow. Alleles responsible for the number of bands are located in other unlinked loci. The gene determining the lack of bands is dominant and epistatic to alleles responsible for band appearance (Lamotte 1954; Cain et al. 1968; Murray 1975; Jones et al. 1977). The distribution of morphs is sympatric and almost every population is variable in shell colour and banding pattern (Jones et al. 1977).

Study area

Individuals of *Cepaea nemoralis* (L.) were collected between April and July 2009 from a population located near the city of Poznań, Wielkopolska, Poland (52°26′N, 16°52′E). The sampling site covered 400 m^2, which is the estimated size of one panmictic unit in *C. nemoralis* (Lamotte 1951). Specimens were collected from a diversified site where vegetation has been spontaneously developing for over 50 years. Our study area was dominated by open habitats that were composed mainly of grasses (about 40 % of the site area) and psammophilic vegetation (about 30 % of the site area) with dwarf everlast [*Helichrysum arenarium* (L.)]. Dark shaded habitats (ca. 30 % of the area) were composed of shrubs, including blackthorn (*Prunus spinosa* L.) and trees such as black locust (*Robinia pseudoacacia* L., Fabaceae) and hedge maple (*Acer campestre* L.). As the collection of snails was random across the sampling site and the percentages of particular morphs occurring in various microhabitats within

the site were similar (chi-square test for the distribution of shell colours: $\chi^2_1=0.02$, $P=0.897$ and banding types: $\chi^2_3=1.21$, $P=0.752$), it is unlikely that any differences among the morphs were caused by microhabitat-related environmental factors. Both avian (*T. merula*) and mammalian predators (*Apodemus* sp.) were observed in the study plot.

Data collection

Visual searching for adult snails was done by an experienced human observer along transects with haphazard sampling. Altogether, 260 adult specimens of *C. nemoralis* were collected. Snails with the evidence of prior predation—with damaged shells and/or scars on the shell were excluded during collection. Shell colour (yellow, pink or brown; Cain and Currey 1963) and the number of bands were recorded. Four types of shell banding were distinguished: (1) mid-banded (banding type 00300, according to Cain and Sheppard 1950, 1954; Fig. 1), (2) three-banded (00345), (3) five-banded (12345) or (4) unbanded (00000). In our study area, all morph types but brown ones were present, resulting in eight different morphs altogether.

Handling of snails and basic measurements

Collected snails were kept in plastic, aerated boxes at 22 °C and humidity of 80–90 % without food (to empty their alimentary canals) for 24 h after the capture. Next, snails were weighed with a scale (to the nearest 0.01 g), individually marked and frozen at −20 °C for 10 days. Then, mortified snails were defrosted at 22 °C for 5–7 h. Shell width and

Fig. 1 Scheme of banding types of *C. nemoralis* morphs. Shell areas subjected to strength measurements are shown on the unbanded morph: *A* labium (usually attacked by mice) and *B* left side of the second whorl (usually broken by birds)

columella height were measured using callipers (0.01 mm accuracy) according to standard methods (Wiktor 2004). Immediately after defrosting, shell strength was measured (with soft tissues present inside the shells) as shell resistance to breakage. The measurements were done with the use of dynamometer FG-5000A (Lutron Electronic Enterprise Co. Ltd, Taipei, Taiwan) to the nearest 0.01 N. A sharp conical tip was mounted on the force gauge, and the device was pushed onto the shell of a stabilised individual until the shell surface broke (Jordaens et al. 2006). After extraction of snail soft tissues, shell wet mass (all fragments) was measured with a scale (to the nearest 0.01 g). Because avian and mammalian predators differ in their manner of breaking and extracting shell contents (Morris 1954; Wolda 1963; Fig. 2), shell strength was measured in two different shell areas (Fig. 1): (1) near the shell apex, on the left side of the second whorl ("avian type") and (2) near the labium, ca. 2 mm above the shell aperture ("mouse type"). Snails from each morphological type were randomly assigned to one of the breakage types (at the apex or labium). Moreover, three calliper measurements (to the nearest 0.01 mm) were taken in different positions around the breakage and the mean was calculated as an estimate of shell thickness (Jordaens et al. 2006). As a result, there were two groups of individuals within each morph: (1) those with shell resistance and thickness measured near the apex and (2) those with both measurements taken above the labium.

Statistical analyses

To compare shell parameters (such as width, mass and columella height) among various morphs, we used two-way ANOVAs followed by Tukey post hoc tests as a post hoc procedure, with shell colour and banding type as factors. Differences in shell thickness were analysed with shell area (apex or labium) as the third factor by three-way ANOVA. Spearman correlations were used to check whether the abovementioned shell features were correlated with one another and with shell strength. A general linear model was used to test the effect of shell colour, banding pattern, shell area (grouping variables), shell thickness (covariate) and their interactions on shell strength (dependent variable). Sequential Bonferroni-corrected Fisher's LSD tests were used
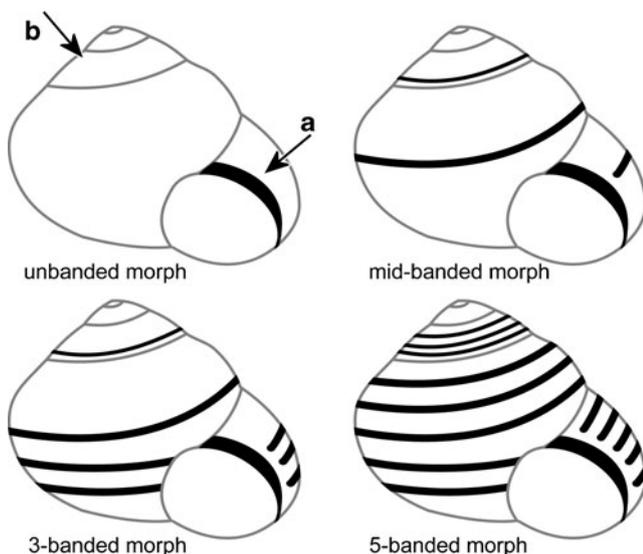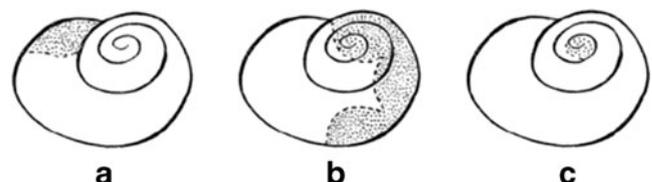

Fig. 2 a–c Shells of terrestrial snails with typical areas (*shaded*) usually damaged by mice (**a**) or birds (**b** and **c**). Occasionally, a shell may show a combination of both types of damage and thus may have been damaged by both predators (after Rosin et al. 2011)

as a post hoc procedure for significant effects of the grouping variables. In the cases of significant interactions of the covariate with the grouping variables, the regression slopes for particular levels of the grouping variables were compared with one another using the procedure described by Sokal and Rohlf (1995). All calculations were carried out by SPSS 19.0 software.

Results

Snail shell traits and their relations

Shell width and thickness were related to banding pattern, with three-banded shells being narrower and unbanded shells thinner than the other morphs (Tables 1 and 2). Moreover, shells were thicker near the labium than at the apex (Tables 1 and 2). Columella height (mean±SE, 12.14±0.04 mm) and shell mass (0.57±0.01 g) (Table 1) did not differ significantly among the studied morphs (Table 2).

Shell strength was positively correlated with shell thickness and mass (Table 3). That is why we selected shell thickness as a covariate for the general linear model to test the effects of snail morphs on shell resistance. Since shell thickness and mass were strongly correlated with each other, there was no need to include both variables into the model. Moreover, columella height was positively related to shell thickness and strength at the apex but not at the labium (Table 3).

Shell strength

Shell strength ranged from 8.1 to 55.00 N, with the mean (±SE) being 22.68±0.85 N and 26.75±0.91 N for the apex and labium, respectively (Fig. 3).

Shells of pink morphs were generally stronger than those of yellow snails (Fig. 3), as shown by a significant colour effect in the general linear model (Table 4). The effect of banding type on shell strength depended on shell area (a significant banding × shell area interaction in the model, Table 4). The area near the apex was strongest in three-banded morphs and weakest in five-banded individuals (Fig. 3). On the other hand, the labium was least resistant to breakage in unbanded snails, whereas its strength did not differ among the other morphs (Fig. 3). The labium was generally more resistant than the apex, though a significant difference between both locations on the shell surface was only found for five-banded morphs (Fig. 3).

Shell resistance was strongly positively related to its thickness, but this relationship varied between shell colours and banding types, as shown by significant colour × thickness and banding × thickness interactions (Table 4). Shell strength of pink snails increased with the increment of shell thickness faster than that of yellow individuals, as indicated by a significant difference between the regression slopes (Fig. 4a). Moreover, the gain in shell strength with the increase in its thickness was greater in banded morphs, with a significant difference between the slopes for three-banded and unbanded individuals (Fig. 4b).

Discussion

We have shown that colour morphs of C. nemoralis significantly differ in shell strength as well as in the magnitude of strength gain per unit of increment of thickness. Shell strength also differed between shell areas usually attacked by birds and mice. Thus, shell strength may be important in determining predator selection among morphs.

Table 1 Mean (± SE) values of columella height, shell width, thickness and mass of C. nemoralis morphs

Morph	Columella height [mm]	Shell width [mm]	Shell mass [g]	Shell thickness [mm]	
				Broken at apex	Broken at labium
Pink					
Unbanded	12.25±0.12	21.30±0.15	0.55±0.02	0.19±0.01	0.17±0.02
Mid-banded	12.09±0.09	21.18±0.11	0.58±0.02	0.20±0.01	0.20±0.01
Three-banded	12.02±0.16	20.87±0.20	0.60±0.03	0.19±0.01	0.24±0.02
Five-banded	12.16±0.13	21.00±0.17	0.60±0.03	0.20±0.01	0.22±0.01
Yellow					
Unbanded	12.18±0.12	21.00±0.15	0.55±0.02	0.16±0.01	0.19±0.02
Mid-banded	12.30±0.12	21.37±0.16	0.56±0.03	0.20±0.01	0.22±0.01
Three-banded	11.99±0.18	20.34±0.23	0.58±0.04	0.21±0.02	0.21±0.02
Five-banded	12.06±0.12	21.23±0.15	0.55±0.02	0.15±0.01	0.22±0.02

Sample sizes of each morph category are presented in Fig. 3

Table 2 Comparisons of shell features among the studied *C. nemoralis* morphs (ANOVA)

Variable	Factor	df	MS	F	P value	Post hoc test
Columella Height	Colour (C)	1	0.000	0.00	0.9816	
	Banding (B)	3	0.410	0.86	0.4636	
	C × B	3	0.379	0.79	0.4987	
	Error	252	0.478			
Shell Width	Colour (C)	1	0.518	0.65	0.4223	
	Banding (B)	3	3.684	4.59	0.0038[a]	0a 1a 3b 5a
	C × B	3	1.825	2.28	0.0803	
	Error	252	0.802			
Shell Mass	Colour (C)	1	0.029	1.43	0.2328	
	Banding (B)	3	0.015	0.73	0.5321	
	C × B	3	0.005	0.24	0.8671	
	Error	250	0.020			
Shell Thickness	Colour (C)	1	0.001	0.42	0.5156	
	Banding (B)	3	0.011	4.43	0.0047[a]	0b 1a 3a 5ab
	Breakage type (BT)	1	0.026	10.22	0.0016[a]	Apex b Labium a
	C × B	3	0.002	0.82	0.4853	
	C × BT	1	0.003	1.16	0.2831	
	B × BT	3	0.005	1.90	0.1298	
	C × B × BT	3	0.005	1.88	0.1327	
	Error	244	0.003			

Groups labelled with the same lowercase letters (a > b) in the last column did not differ from one another (post hoc Tukey test). Numbers 0–5 refer to various banding types (unbanded, mid-banded, three-banded and five-banded, respectively)

[a] Significant effects

Strength of external skeletons has been shown to be a principal anti-predator defence for molluscs. For example, European oystercatchers *Haematopus ostralegus* preferentially selected thin-shelled mussels *Mytilus edulis* (Durell et al. 1984; Nagarajan et al. 2002). Moreover, the increase in shell thickness is a known defence mechanism against shell-crushing predators in both aquatic and land snails (Lewis and Magnuson 1999; Allen 2004; Dalziel and Boulding 2005). However, only Quensen and Woodruff (1997) suggested that predator selectivity could be based on the shell strength of a land snail.

We have shown that shell strength of *C. nemoralis* strongly depended on shell thickness, which was also suggested for *C. nemoralis* by Jordaens et al. (2006) as well as for other gastropods, such as *Littorina pallescens* (Cook and Kenyon 1993) and *Cerion* sp. (Quensen and Woodruff 1997). We show that pink morphs have more resistant shells than yellow ones. Jordaens et al. (2006) did not find significant differences between these *C. nemoralis* morphs, perhaps due to the differences in shell areas subjected to measurements or techniques of breaking shells since shell thickness was similar in both studies. Moreover, Jordaens et al. (2006) did not consider banding pattern of studied morphs which may have contributed to the greater variation within their colour categories. In our study, darker (pink) morphs showed higher increment in shell strength with the increase in shell thickness than yellow individuals did, which may explain their greater resistance. Banded forms (particularly three-banded ones) also showed higher increase in shell strength with shell thickness than unbanded individuals. This relationship is independent of differences in absolute shell dimensions among morphs, demonstrating that the banding pattern in itself affects shell resistance. Dark bands are present in all shell layers (Emberton 1963). The crushing resistance of a molluscan shell depends mainly on its middle calcareous prismatic layer (Le Rossignol et al. 2011); thus, the strengthening role of the dark bands present in this layer is likely.

Table 3 Spearman correlation coefficients among the studied shell parameters

	H	W	Ta	Tl	M
Columella height (H)					
Shell width (W)	0.49***				
Shell thickness at the apex (Ta)	0.33***	0.12			
Shell thickness at the labium (Tl)	−0.04	−0.10			
Shell mass (M)	0.30***	0.19*	0.77***	0.72***	
Shell strength at the apex	0.27*	0.12	0.72***		0.79***
Shell strength at the labium	−0.09	−0.16		0.73***	0.61***

*P<0.05, ***P<0.001 (statistically significant)

Fig. 3 Mean shell strength (±SE) of the studied morphs of *C. nemoralis*. Numbers of particular morphs used in the study are shown above the plot. *Numbers 0–5* below the bars indicate banding pattern: unbanded, mid-banded, three-banded and five-banded morphs, respectively. The banding types labelled with the same letters on the bars did not differ significantly from one another (within the same shell colour and area) (a > b > c). *Asterisks* indicate banding types for which significant differences between shell areas (apex vs. labium) were observed. Sample sizes are given on the top of each bar
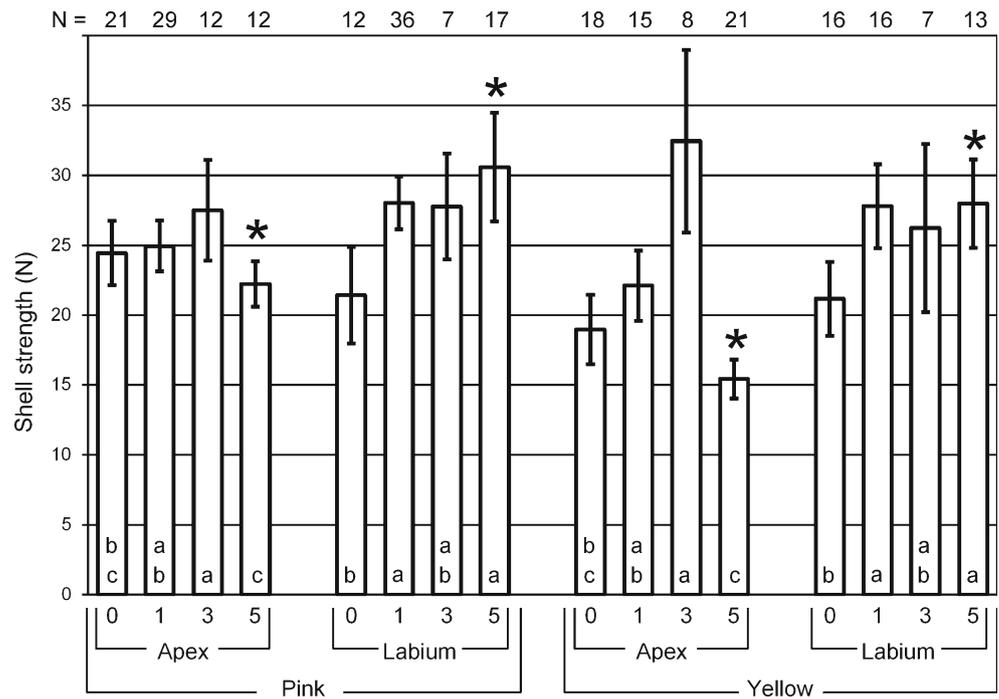
To our knowledge, there are no precise data on heritability of shell strength in snails. However, a study on marine gastropod *Bembicum vittatum* showed a strong genetic basis of its shell morphology (Parsons 1997) which is an important factor affecting shell strength (DeWitt 2000; Rundle and Brönmark 2001). On the other hand, shell strength could be strongly shaped by the environment, e.g. calcium availability. Nevertheless, as our snails were randomly collected and randomly distributed within one panmictic unit for this species (Lamotte 1951), the environmental impact on various morphs in our study was similar. Thus, we probably observed the genetic variability in shell strength among the

morphs. However, our results should be treated with caution since we studied only one population and did not account for such factors as shell strength variation in different *C. nemoralis* colonies or across the lifespan of individuals. Nevertheless, we did demonstrate that a significant relationship between shell colour morph and strength can exist in *C. nemoralis* snails at least at a local scale.

The shell part usually attacked by birds (near the apex) was generally less resistant to crushing than that usually gnawed by mice (labium). Thrushes, specialising in consuming snails, hold a snail in their beak and hit it against an "anvil" (Morris 1954) trying to break various shell parts until

Table 4 General linear model of the effects of shell colour, shell banding pattern, breakage type (grouping variables), shell thickness (covariate) and their interactions on shell strength of *C. nemoralis*

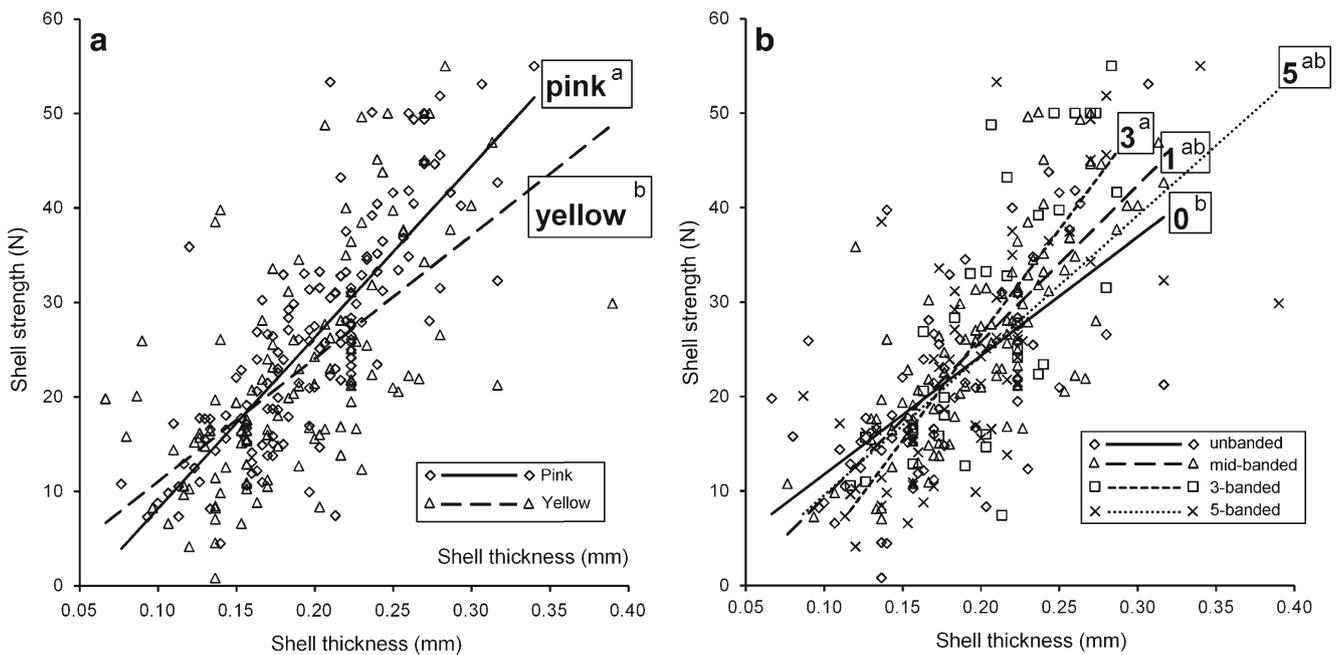| Variable	df	MS	F	P value
Colour (C)	1	603.0	9.8	0.0020[a]
Banding (B)	3	256.5	4.2	0.0068[a]
Shell area (SA)	1	21.9	0.4	0.5524
Thickness (T)	1	13373.3	216.4	0.0000[a]
Interactions				
C × B	3	137.2	2.2	0.0866
C × SA	1	82.5	1.3	0.2490
B × SA	3	359.9	5.8	0.0007[a]
C × B × SA	3	24.2	0.4	0.7587
C × T	1	768.8	12.4	0.0005[a]
B × T	3	316.7	5.1	0.0019[a]
SA × T	1	16.4	0.3	0.6074
Error	238	61.8		

[a] Significant effects

Fig. 4 Relationships between shell thickness and strength for various shell colours (**a**) and banding types (**b**) in *C. nemoralis*. The slopes of lines labelled with the same superscript letters did not differ significantly from one another (a > b)

they find the thinnest area. By contrast, mice, having relatively small jaws and mouth gape, can only access a shell at the aperture, so the strengthening of this area may help snails avoid mice predation.

In the study by Rosin et al. (2011) mice preyed most heavily on yellow unbanded and one-banded morphs, which in the present study had the weakest shell areas near the aperture. Mice use mainly olfactory stimuli in foraging (Allen 2004). Thus, their predation on snails is probably based on trial and error resulting in the highest feeding rate on snails with weak shells. This, together with the differences in shell strength among colour morphs found in the present study, could explain the selectivity of mice towards particular morphs observed by Rosin et al. (2011). Other factors than shell strength may affect mouse predation on *Cepaea* morphs, e.g. associations of morphs and mice to various (micro)habitats (Silvertown et al. 2011). Moreover, mouse predation may be different on juvenile snails (not studied). However, it is unlikely that any mouse selectivity based on juvenile shell strength occurs since juvenile shells are thinner and less resistant to breakage than adult shells (Jordaens et al. 2006) and usually are swallowed in whole. Nevertheless, mice belong to the most important predators hunting adult *C. nemoralis* (Allen 2004; Rosin et al. 2011) and almost 60 % of colonies show traces of mouse predation on adult snails (Rosin's personal observation). On the other hand, birds, having greater abilities to crush shells and being visual predators, may depend mainly on morph conspicuousness (e.g. Cain and Sheppard 1954; Allen and Clarke 1968; Surmacki et al. 2013).

Many factors, including habitat heterogeneity, migration rate, landscape structure etc., might have also influenced the maintenance of shell polymorphism in *Cepaea*. The open question is how important the individual factors are. We consider predation as one of the factors that require more attention than it has been given to date in *Cepaea*. Many questions about ultimate and proximate factors shaping differential predator pressure on *Cepaea* morphs are unresolved. Our results suggest that shell crushing resistance may be a proximate factor of differential predatory pressure on *Cepaea* morphs, justifying future studies on the direct effect of variable shell strength of *C. nemoralis* morphs on predator selectivity.

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