
Differences in predatory pressure on terrestrial snails by birds and mammals

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The evolution of shell polymorphism in terrestrial snails is a classic textbook example of the effect of natural selection in which avian and mammalian predation represents an important selective force on gene frequency. However, many questions about predation remain unclear, especially in the case of mammals. We collected 2000 specimens from eight terrestrial gastropod species to investigate the predation pressure exerted by birds and mice on snails. We found evidence of avian and mammalian predation in 26.5% and 36.8% of the shells. Both birds and mammals were selective with respect to snail species, size and morphs. Birds preferred the brown-lipped banded snail *Cepaea nemoralis* (L.) and mice preferred the burgundy snail *Helix pomatia* L. Mice avoided pink mid-banded *C. nemoralis* and preferred brown mid-banded morphs, which were neglected by birds. In contrast to mice, birds chose larger individuals. Significant differences in their predatory pressure can influence the evolution and maintenance of shell size and polymorphism of shell colouration in snails.

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1. Introduction

The evolution of shell polymorphism in the terrestrial brown-lipped banded snail, *Cepaea nemoralis* (L.), is an ideal model for studies on the effect of natural selection on gene frequency (Davison 2002). Variation in colour and banding pattern of the shells in *Cepaea* populations has been the subject of many studies for over 100 years (e.g. Sheppard 1951; Cain and Sheppard 1954; Cain and Currey 1967; Allen *et al.* 1988). However, the origin and maintenance of this variability is still unclear (Cook 2005). Among several hypotheses attempting an explanation of this phenomenon, selective predation is the most probable (Punzalan *et al.* 2005). Avian predation on snail populations is a common and well-known phenomenon

(e.g. Morris 1954; Cameron 1969). Most previous studies (Sheppard 1951; Cain and Sheppard 1954; Jones *et al.* 1977; Cook 2005) focused on thrushes (*Turdus* spp.) as the species eating terrestrial gastropods, but the snail contribution to these predators' diet is still unclear. Some authors suggested that snails are only an alternative source of energy for thrushes (e.g. Wolda 1963; Cain and Currey 1967; Cameron 1969), whereas others have stated that terrestrial gastropods are the main element of the diet of thrushes (Richards 1977; González-Solis *et al.* 1996).

Birds are not the only vertebrates that hunt molluscs. One of the most important predators of terrestrial gastropods may be rodents, especially mice (Allen 2004). However, information about their selective feeding and their effects on

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snail populations is scarce. Earlier studies mention small mammals as predators of terrestrial molluscs (e.g. Cain and Currey 1967; Baur and Baur 1993; Allen 2004) or list snail species as a potential food source for mammals (Allen 2004). However, as far as we are aware, there is only one study that tested the influence of small mammals on morph frequency and size of various snail species (Moreno-Rueda 2009).

Shell size is a feature of snails that is under strong selection. Several investigations showed that predators chose the energetically most profitable prey from among available ones (e.g. Stephens and Krebs 1986; Quensen and Woodruff 1997; Norris and Johnstone 1998). Thus, optimal size of shells for predators should be small enough to be easy to break and large enough to provide a worthwhile portion of food (Reed and Janzen 1999). To date there have been no attempts to investigate the effects of predator selectivity on shell size in communities composed of more than two snail species.

There is evidence that selective feeding by birds and mammals can actively maintain polymorphism for shell and body colourations in terrestrial molluscs by their capturing common morphs and overlooking rare ones ('apostatic selection', Allen and Clarke 1968; Clarke 1969). However, studies investigating and comparing their simultaneous effect on terrestrial gastropod communities composed of different species have not been published yet. Therefore, the aim of the current study was not only an investigation of avian and mammalian food preference toward particular snail species, morphs and sizes, but also an attempt to determine their influence on investigated snail populations and to find out whether they operate via hierarchical selectivity.

2. Materials and methods

2.1 Study area

Research was carried out between April and June 2005 in Poznań, Wielkopolska, Poland (52°20' N, 16°54' E). Specimens were collected from a grassland site located in the suburbs, where vegetation has been spontaneously developing for over 50 years. Apart from intentionally introduced black locust (*Robinia pseudoacacia* L., Fabaceae), there were also anemochoric species, such as hedge maple (*Acer campestre* L.), sycamore maple (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), and in the field layer, there were wood anemone (*Anemone nemorosa* L.) and lesser celandine (*Ficaria verna* Huds.). There was also psammophilic vegetation (about 20% of the site area) with dwarf everlast [*Helichrysum arenarium* (L.)] diversified by shrubs including blackthorn (*Prunus spinosa* L.). Therefore, our study area was dominated by dark, shaded

habitats that were composed mainly of shrubs and young trees.

2.2 Data collection

In the study plot, there were two avian predator species [the blackbird (*Turdus merula* L.) and the song thrush (*T. philomelos* Brehm)], and one main mammalian species [the wood mouse (*Apodemus sylvaticus* L.)] as determined by directional observations.

Visual searching of both living snails and empty shells was done by a well-trained human observer, and altogether 2000 shells of adult snails were collected. They belonged to eight terrestrial snail species: the copse snail (*Arianta arbustorum* L.), the burgundy snail (*Helix pomatia* L.), the brown-lipped banded snail (*Cepaea nemoralis* L.), the white-lipped banded snail [*Cepaea hortensis* (Müll.)], the bush snail [*Bradybaena fruticum* (Müll.)], the heath hellicelid [*Helicella obvia* (Menke)], the amber Snail [*Succinea putris* (L.)] and the western glass snail [*Vitrina pellucida* (Müll.)]. However, the last two species occurred only in very small numbers ($N < 4$ individuals), and were, therefore, excluded from the main analyses (the sample size used in the analyses was 1995 individuals; see [supplementary material](#)).

Most of the predated shells were damaged to a high degree. Thus, only shell breadth and columella height were measured with callipers to the nearest 0.01 mm (*C. hortensis* shells damaged by both bird and mice were not measured because of the high degree of shell damage). In the case of *C. nemoralis* and *C. hortensis*, shell colour (yellow, pink or brown; Cain and Currey 1967) and the number of bands were also recorded. Three types of shell banding were determined: (1) mid-banded (banding type 00300, according to Cain and Sheppard 1950, 1954); (2) multi-banded (i.e. more than one band), including the following banding types: 00345 (three bands) and 12345 (five bands); or (3) unbanded (00000).

2.3 Identification of predation type

Marks left on shells by avian and mammalian predators are quite easily distinguishable due to differences in their location on the shell and manner in which the shell contents were extracted (figure 1) (Morris 1954; Wolda 1963; Tryjanowski and Olborska unpublished observations). Thus, the type of damage to shells was attributed to birds based on marks of strikes on the left part of the last whorl, to mice based on marks of tooth bites on the aperture or to both of them. Ambiguous marks on the shells were assessed with a magnifying glass. In some cases, a high degree of damage to some *Cepaea* shells made it impossible to identify the snail species or to

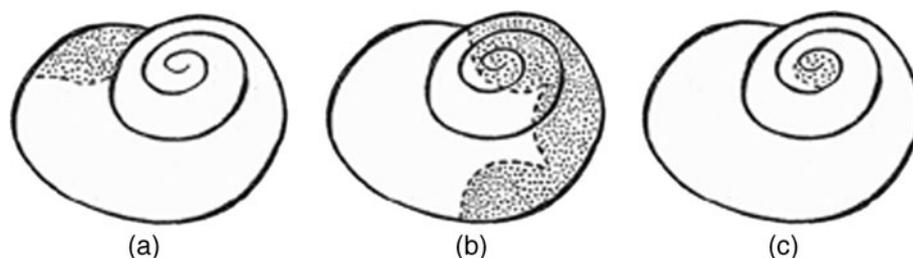


Figure 1. Shells of terrestrial snails with typical damage (shaded areas) usually damaged by mice (a) or birds (b, c). Occasionally, a shell may show a combination of both types of damage and, thus, may have been damaged by both predators.

determine whether two shell fragments were parts of the same shell. Therefore, only damaged shells with fragments of the labium that was large enough to unequivocally identify the snail species were used (Sheppard 1951).

2.4 Data analysis

In order to show avian or mammalian preference toward particular species, two commonly used selectivity indices were used. The first one was *D*, the selectivity index (Jacobs 1974), calculated as

$$D = (r - p) / (r + p - 2rp),$$

in which *r*=taxon ratio in the food and *p*=taxon ratio in the environment.

The index *D* can take values from -1 (total avoidance) to +1 (total preference). Values close to zero (from -0.1 to +0.1) indicate a lack of relationship. In the case of *C. nemoralis* and *C. hortensis*, the index *D* was also calculated for all nine (three colour × three banding) morph categories.

The second selectivity index was the Savage's index (Savage 1931). It was determined as

$$W = A/T,$$

in which *A*=taxon ratio in the environment and *T*=taxon ratio in the food.

The values of the index *W* vary between 0 and ∞, where 1 means no preference of prey and values lower and higher than 1 indicate avoidance and preference, respectively. This index was added because it is possible to test its statistical significance with a Chi-square test (Manly *et al.* 1993) after applying Bonferroni adjustment (α [significance level]/number of categories; Oscoz *et al.* 2006).

Calculations were conducted using the package SPSS version 13 for Windows (SPSS 2003). Parametric tests (two sample *t*-test and ANOVA) were used because the data were approximately normally distributed (as indicated by the

Kolmogorov–Smirnov tests) and variances were homogeneous (as indicated by the Levene's tests).

3. Results

3.1 Relative numbers and quantitative relationships of snail species in the study area

The structure of terrestrial gastropod communities was dominated by three species. *C. nemoralis* was the species represented by the highest number (36.6%) of all collected specimens (live snails as well as empty shells). *H. pomatia* and *A. arbustorum* were also important species in the snail community (27.2% and 26.8%, respectively). The remaining species (*C. hortensis*, *B. fruticum*, *H. obvia*, *S. putris* and *V. pellucida*) constituted together 9.4% of all collected specimens.

3.2 Predation pressure on snails

Almost 65% of the sampled shells showed marks of avian and/or mammalian predation. From among 1995 analysed shells, 736 (36.8%) had marks left by mice. Damage caused by birds was found in 530 (26.5%) shells, and 40 (2.0%) showed marks left by birds and mice. Among all the shells damaged by birds (*N*=530), 82.3% were *C. nemoralis*. *H. pomatia* shells constituted the largest percentage (47.0%) of all shells predated by mice (*N*=736) (figure 2).

3.3 Avian and mammalian food preference toward investigated snail species

Birds and mice differed significantly in preference toward particular snail species. Birds selected *C. nemoralis* most frequently and avoided *H. pomatia*, *B. fruticum*, *H. obvia* and *A. arbustorum* (table 1). Mice neglected *C. nemoralis* and preferred *H. pomatia* and *B. fruticum*, but showed no preference for *A. arbustorum*, *C. hortensis* and *H. obvia* (table 1).

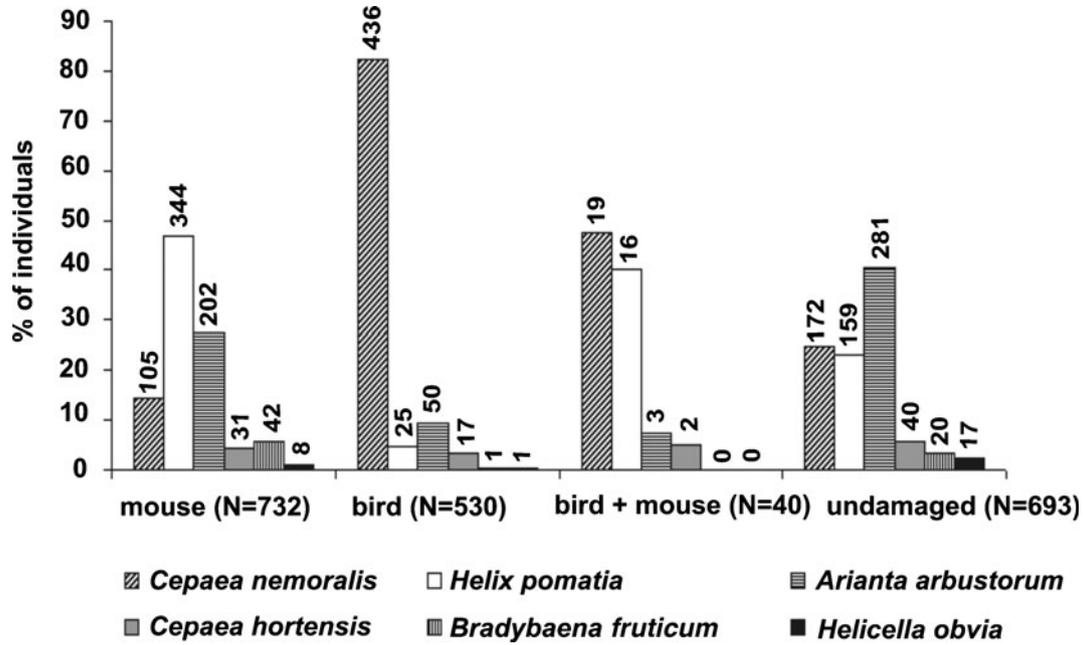


Figure 2. Percentage of damage type observed in a variety of terrestrial snail species. Key: mouse=shells predated by mice; bird=shells predated by birds; bird+mouse=shells predated by both. Percentage of individuals presented on y-axis totals to 100% within damage type. Solid numbers of the shells are given on the top of each column.

3.4 Relationship between shell size and predation type

In all species there was a strong positive correlation between shell breadth and columella height (*r* between 0.762 and 0.933, *P*<0.001 for all species).

ANOVA revealed significant differences between all four damage classes (including undamaged shells) for shell breadth and columella height in *C. nemoralis*, *H. pomatia*, *A. arbustorum*, and *C. hortensis* (table 2). Multiple

comparison tests revealed which damage classes differed significantly (table 3).

3.5 Avian and mammalian preference toward *Cepaea* spp. morphs

Index *D* showed that mice avoided pink mid-banded forms of *C. nemoralis* and preferred yellow mid-banded individuals and also brown mid-banded morph, which was entirely

Table 1. Preferences of mice and birds toward particular species of snails (*N*=1995) determined by *D* and Savage’s indices. Savage’s index tested for significance with Chi-square test

Species	Mice			Birds			Mouse+bird		
	Index <i>D</i>	Savage’s index	Chi-square (<i>P</i> -value)	Index <i>D</i>	Savage’s index	Chi-square (<i>P</i> -value)	Index <i>D</i>	Savage’s index	Chi-square (<i>P</i> -value)
<i>Cepaea nemoralis</i>	-0.552	0.393	157.38 (<0.001)	0.778	2.242	473.86 (<0.001)	0.219	1.295	2.01 (0.156)
<i>Helix pomatia</i>	0.406	1.723	143.62 (<0.001)	-0.767	0.173	135.90 (< 0.001)	0.280	1.467	3.27 (0.071)
<i>Arianta arbustorum</i>	0.018	1.027	0.20 (0.657)	-0.558	0.351	81.98 (< 0.001)	-0.638	0.279	7.64 (0.006)
<i>Cepaea hortensis</i>	-0.033	0.939	0.13 (0.719)	-0.175	0.711	2.09 (0.148)	0.054	1.108	0.02 (0.882)
<i>Bradybena fruticum</i>	0.273	1.708	12.77 (<0.001)	-0.897	0.056	16.41 (< 0.001)	-1.000	0	1.39 (0.238)
<i>Helicella obvia</i>	-0.089	0.839	0.25 (0.616)	-0.750	0.145	5.12 (0.024)	-1.000	0	0.53 (0.467)

Note that mouse+bird means shell damaged by both predators.

Statistically significant differences (after Bonferroni adjustment) where when *P*<0.010 (bold).

Table 2. Mean values (\pm standard errors) of shell breadth and columella height of different snail species and tests of differences between damage classes (including undamaged shells) in these shell features (one-way ANOVA or *t*-test)

Species	Damage class	Breadth		Columella height	
		Test	Mean (\pm SE)	Test	Mean (\pm SE)
<i>Cepaea nemoralis</i>	Mouse		17.872 (\pm 0.18)		10.804 (\pm 0.12)
	Bird	$F_{3,385}=29.26$	19.359 (\pm 0.09)	$F_{3,326}=34.49$	12.200 (\pm 0.08)
	Bird+mouse	$P<0.001$	19.196 (\pm 0.01)	$P<0.001$	12.209 (\pm 0.08)
	Undamaged		20.549 (\pm 0.08)		12.764 (\pm 0.05)
<i>Helix pomatia</i>	Mouse		32.149 (\pm 0.24)		22.775 (\pm 0.20)
	Bird	$F_{3,446}=10.44$	36.011 (\pm 0.07)	$F_{3,500}=16.40$	26.934 (\pm 0.05)
	Bird+mouse	$P<0.001$	33.640 (\pm 0.10)	$P<0.001$	22.628 (\pm 0.08)
	Undamaged		34.483 (\pm 0.19)		25.375 (\pm 0.16)
<i>Arianta arbustorum</i>	Mouse		18.561 (\pm 0.10)		11.661 (\pm 0.07)
	Bird	$F_{3,459}=6.74$	19.365 (\pm 0.07)	$F_{3,500}=8.13$	12.259 (\pm 0.06)
	Bird+mouse	$P<0.001$	20.810 (\pm 0.02)	$P<0.001$	12.787 (\pm 0.03)
	Undamaged		19.368 (\pm 0.08)		12.288 (\pm 0.05)
<i>Cepaea hortensis</i> *	Mouse	$F_{2,74}=9.04$	17.704 (\pm 0.20)	$F_{2,74}=8.96$	10.805 (\pm 0.12)
	Bird	$P<0.001$	19.770 (\pm 0.17)	$P<0.001$	12.290 (\pm 0.10)
	Undamaged		19.009 (\pm 0.15)		11.559 (\pm 0.12)
<i>Bradybena fruticum</i>	Mouse	$t_{60}=0.31$	13.530 (\pm 0.38)	$t_{62}=0.34$	7.690 (\pm 0.34)
	Undamaged	n.s.	13.800 (\pm 0.46)	n.s.	7.910 (\pm 0.30)
<i>Helicella obvia</i>	Mouse	$t_{23}=3.18$	11.360 (\pm 0.11)	$t_{23}=1.59$	4.280 (\pm 0.09)
	Undamaged	$P=0.004$	12.540 (\pm 0.20)	n.s.	4.570 (\pm 0.09)

*Note that in the case of *C. hortensis* shells damaged by both bird and mice, measurements of shell breadth and columella height were not done because of the high degree of shell damage.

avoided by birds (table 4). Brown unbanded individuals were also neglected by birds (table 4). There were no significant bird preferences toward yellow unbanded and mid-banded, pink multi-banded and brown multi-banded morphs ($-0.1 \leq D \leq 0.1$, table 4). In *C. hortensis*, birds preferred pink multi-banded forms, whereas mice avoided yellow unbanded morphs (table 4).

Table 3. Significant differences between damage categories in shell breadth and columella height (ANOVA and *post hoc* Scheffe's tests)

Species	Comparison	Shell feature	
		Breadth	Columella height
<i>Cepaea nemoralis</i>	M vs U	$P<0.001$	$P<0.001$
	M vs B	$P=0.001$	$P<0.001$
	B vs U	$P<0.001$	–
<i>Helix pomatia</i>	M vs U	$P<0.001$	$P<0.001$
<i>Arianta arbustorum</i>	M vs U	$P=0.001$	$P<0.001$
<i>Cepaea hortensis</i>	M vs B	–	$P=0.001$

M, shells damaged by mice; B, shells damaged by birds; U, undamaged shells.

An apparently very strong preference of both birds and mice (with shells having marks left by both predators) toward brown mid-banded forms of *C. nemoralis* must be treated with caution because the frequency of that morph in the sampled *C. nemoralis* was very low and even one individual could have changed the value of the selectivity indices (see supplementary material). Overall, the indices did not always give consistent results. This might be due to the fact that the *P*-value of the chi-square test of Savage's index strongly depends on sample size (Zar 2010). In contrast, the selectivity index *D* is robust with respect to differences in sample size, and in small samples it may give more accurate estimates of selectivity (Jacobs 1974).

4. Discussion

4.1 Avian and mammalian predatory pressure on snails

As far as we are aware, this is the first study that (i) combines information on *C. nemoralis* with that on other co-existing snail species and on predatory pressure exerted on them and (ii) focuses on different predatory types. However, prior to a detailed discussion of the findings, it is worth noting a potential imperfection in the sampling

Table 4. Food preference of mice and birds toward particular morphs of *Cepaea nemoralis* – upper panel ($N=732$) and *Cepaea hortensis* – lower panel ($N=90$), determined by D and Savage's selectivity indices

Morph	Mice			Birds			Mouse+bird*		
	Index D	Savage's index	Chi-square (P -value)	Index D	Savage's index	Chi-square (P -value)	Index D	Savage's index	Chi-square (P -value)
<i>Cepaea nemoralis</i>									
Yellow mid-banded	0.320	1.877	2.97 (0.085)	-0.090	0.839	0.41 (0.520)	0.672	4.445	8.31 (0.004)
Yellow>1-band	-0.038	0.953	0.14 (0.706)	0.106	1.135	4.89 (0.027)	-0.140	0.832	0.33 (0.565)
Yellow unbanded	0.094	1.162	0.64 (0.424)	-0.009	0.985	0.02 (0.884)	0.069	1.117	0.06 (0.806)
Pink mid-banded	-1.000	0.000	0.72 (0.395)	-0.198	0.672	0.32 (0.570)	-1.000	0.000	0.13 (0.718)
Pink>1-band	-0.125	0.822	1.06 (0.302)	0.000	1.000	0.00 (0.998)	-0.093	0.866	0.11 (0.740)
Pink unbanded	0.043	1.084	0.05 (0.825)	-0.153	0.746	1.84 (0.175)	-0.082	0.856	0.03 (0.872)
Brown mid-banded	0.557	3.486	1.78 (0.182)	-1.000	0	1.19 (0.274)	0.906	19.263	17.36 (<0.001)
Brown>1-band	-0.049	0.909	0.03 (0.867)	0.047	1.095	0.13 (0.721)	-1.000	0.000	0.62 (0.432)
Brown unbanded	0.061	1.124	0.07 (0.789)	-0.520	0.325	8.79 (0.003)	-1.000	0.000	0.84 (0.359)
<i>Cepaea hortensis</i>									
Yellow mid-banded	0.000	0.000	–	0.000	0.000	–	0.000	0.000	–
Yellow>1-band	0.381	1.198	2.84 (0.092)	-0.241	0.840	1.01 (0.315)	-0.400	0.714	0.38 (0.537)
Yellow unbanded	-0.455	0.435	2.82 (0.093)	0.037	1.059	0.02 (0.897)	0.556	2.250	0.89 (0.345)
Pink>1-band	-0.017	0.968	0.00 (0.973)	0.589	3.529	3.75 (0.053)	-1.000	0.000	0.07 (0.793)
Brown unbanded	-1.000	0.000	0.35 (0.555)	-1.000	0.000	0.19 (0.662)	-1.000	0.000	0.02 (0.881)

Savage's index was tested for significance with Chi-square test and was statistically significant (after Bonferroni adjustment) when $P < 0.006$ (bold).

*Mouse+bird means shell damaged by both predators.

methodology. It is possible that some shells may have been overlooked during sampling because of differences in their conspicuousness. It is necessary to consider that some species and morphs are overlooked more readily than others because of better camouflage (Cain and Sheppard 1954; Wolda 1963). Thus, it is possible that brown morphs of the genus *Cepaea*, which are more cryptic to the human eye than yellow or pink morphs, could have been overlooked (Slotow et al. 1993). This may have led to a biased selection by the researcher, which could skew the assessment of avian and mammalian preference toward particular species and morphs. In addition, small snail species and juvenile forms might be swallowed whole by predators (González-Solis et al. 1996; Allen 2004). Information about such behaviours was not obtained in this study and, therefore, was not included in our analyses. Additionally, large shells are easier to find than small ones. Thus, findings about predator preferences with respect to shell size could have been overestimated. Also, contribution of the damaged shells to the number of collected shells might have been overestimated because they are usually located in more prominent sites than undamaged shells (Tryjanowski and Olborska unpublished observations). However, it is important to note that such possible methodological flaws do not

explain the differences found between shells predated by birds and mammals as well as undamaged shells.

Birds and mice were the most prominent predators eating snails in the study area. The difference in food preference between these two types of predators was very clear. Their food niches also overlapped partially – shells belonged to *C. nemoralis* were predated by both birds and mice. However, preferences for particular snail species, morphs and size classes in the predators' diet was obvious.

The results of our study are consistent with those in the literature on thrush diet composition (Wardhaugh 1984; Allen 2004). In the study area, the most frequent snail species eaten by birds was *C. nemoralis*. However, *C. hortensis* and *A. arbustorum*, mentioned in the literature on avian food as frequently as *C. nemoralis*, contributed merely 3.2% and 9.4%, respectively, of the bird damaged shells. In our study, thrushes clearly preferred *C. nemoralis*. This result confirmed the observations by other authors that thrushes eat a higher number of *C. nemoralis* than would be expected if feeding were random (Bantock and Bayley 1973). In contrast, the strong avian avoidance of *H. pomatia* and *A. arbustorum* might result from the fact that brown snails are more cryptic and, thus, more easily overlooked by birds that use visual stimuli (Slotow et al. 1993). The

differences in the number of predated individuals between *C. nemoralis* and *A. arbustorum* might also reflect the difference in behaviour between these two species. Cameron (1969) found that *C. hortensis* (and probably also *C. nemoralis*) were in the habit of climbing up plants, whereas *A. arbustorum* spent most of the time close to the ground. This behaviour might alter the probability of being noticed and eaten by birds.

In the case of mice, our findings are also consistent with those in the literature on their food composition (Allen 2004). *H. pomatia* and *A. arbustorum* were the species eaten most frequently by mice. In contrast to thrushes, mice showed a strong preference for *H. pomatia* and avoidance of *C. nemoralis*. Unfortunately, to date no other investigations on mouse preference for snail species has been undertaken. The minor contribution of *C. nemoralis* in the mice diet might be connected to the previously mentioned tendency of that snail species to climb plants (Cameron 1969). Mice move and search for food mainly on the ground, and therefore snails that stay at a higher level are less exposed to mouse predation.

However, predator preferences for snail species might be strongly influenced by the size of the different species. Therefore, it is essential to clarify predator selection in respect of intra-species size patterns.

4.2 Preferences toward snail size

Birds tend to choose large, rather than small snails of a particular species, presumably because of their higher food value. In the literature, there are inconsistencies with respect of such preferences in birds, with some authors reporting a preference for averaged-size snails (Reed and Janzen 1999) and others reporting a preference for above average-sized snails (Bourne 1993; Allen 2004). For example, the snail kite [*Rostrhamus sociabilis* (Vieillot)] consistently chose larger-than-average golden apple snail [*Pomacea dolioides* (Reeve)] individuals (Bourne 1993). The song thrush preferred mature *A. arbustorum* rather than juveniles (Allen 2004). Song thrushes preying upon sympatric populations of *C. nemoralis* and *C. hortensis* usually preferred the former, larger species, and when both snail species were found together, birds chose larger rather than smaller individuals irrespective of the snail species (Bantock and Bayley 1973).

However, in our study, the song thrushes ate larger *C. hortensis* and smaller *C. nemoralis*; thus, they generally preferred medium-sized snails. As visual predators, the song thrushes and the blackbirds might operate using a 'search image' (Tinbergen 1960; Punzalan *et al.* 2005). If the bird has a built-in concept of an 'ideally sized' snail, individuals that fall outside this size range might have greater chances of surviving preferentially (Bantock and Bayley 1973). In addition, small snails may be overlooked because they are less conspicuous than larger ones.

Mice, which, like most mammals, hunt using mainly olfactory stimuli (Allen 2004) probably do not select snails visually. In our study area, mice showed clear preferences towards a particular size class consisting of small individuals. This probably is so because larger shells require more time and energy to break in order to extract the soft tissues (Reed and Janzen 1999). Larger snails are usually more difficult to handle than smaller ones, and their shells are thicker and mechanically more resistant to damage (Jordaens *et al.* 2006). For mice, which use their teeth to extract the soft tissues from the snail shell, a snail shell may be more difficult to handle the larger and harder it is. Mice preference was expressed in both the columella height and shell breadth of all investigated snail species. Mice probably do not actively search for snail prey (Tryjanowski and Rosin unpublished observations), but snails of different age, size and colouration classes may differ in their predator avoidance behaviour and in their habitat choice.

The difference between birds and mammals in their selectivity of snail size may result from the fact that *T. merula* and *T. philomelos*, the two avian predators in our study area, are larger than mice. Moreover, jaw size and mouth gape of mice may limit their ability to handle large snails. Thus, big snail shells are probably difficult to break into for mice, whereas small snails are not profitable for birds.

Finally, selective predation on prey size by birds and mice exerts considerable pressure on snail populations. Cook and O'Donald (1971) showed that the absence of predators from some parts of the range of *C. nemoralis* may allow the evolution of large-shelled forms in those areas.

4.3 Preference toward particular morphs of *Cepaea* spp.

Birds are supposed to be the main selective agent for the evolution of cryptic colours and other anti-predator adaptations (Allen 2004). Selection with respect to shell colour in polymorphic populations of *Cepaea* spp. may be strong especially in the case of birds, which are visual predators and show a tendency to choose forms that are more conspicuous (e.g. Sheppard 1951; Cain and Sheppard 1954; Slotow *et al.* 1993). Therefore, thrushes were expected to show the most striking differences in morph preferences for *C. nemoralis* and *C. hortensis*. We expected that birds will predate most heavily on yellow morphs, which were the most conspicuous *Cepaea* specimens in our study area. However, in most cases birds showed no preferences with respect to colour or banding pattern. Actually, birds slightly avoided the yellow unbanded morphs of *C. hortensis*, and also showed a noticeable avoidance of brown *C. nemoralis* individuals. The minimal contribution of brown morphs to the avian diet in the study

area may be explained by the fact that dark shells are the most cryptic ones and, thus, are best camouflaged in shaded habitats (Cain and Sheppard 1954; Cain and Currey 1967). Otherwise, colour or banding pattern may be unlikely to have a significant influence on prey choice in mice. However, Goodhart (1987) suggested that mice can distinguish dark from light colours and, thus, may be able to distinguish different banding patterns. There is also evidence for colour-tone-based visual selection in rabbits [*Oryctolagus cuniculus* (L., 1758)] (Cain 1953). Visual selection, if it exists in mammalian predators, may be based only on tone perception (Goodhart 1987; Allen 2004).

The hypothesis that predation by mice could be selective with respect to shell colour and banding pattern is controversial. Some investigations indicated that such preferences do not exist in mice (Slotow *et al.* 1993). However, we found that mice preferred yellow *Cepaea* individuals, which is consistent with suggestions that mice choose yellow morphs particularly in dark habitats (Bengtson *et al.* 1976). Studies on the influence of soil colour and its structure on visual selection by mice might confirm our suggestion of selective predation by colour contrast. However, some differences between birds and mammals in morph preferences may be explained by the fact that different *Cepaea* morphs have different behaviours and may use microhabitats differentially (Jones 1982). Also, different microhabitats might be used with varying intensity by the two predators.

5. Conclusions

Both birds and mammals are selective with respect to snail species, size and morphs. Significant differences in avian and mammalian predatory pressure on terrestrial snail communities can influence the composition of snail communities as well as the evolution and maintenance of shell size and polymorphism for shell colouration.

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