Shell size differences in *Helix lucorum* Linnaeus, 1758 (Mollusca: Gastropoda) between natural and urban environments

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Abstract: *Helix lucorum* Linnaeus, 1758 is a large helicid snail widespread in Georgia. While its occurrences are mainly associated with human activity, it is frequently impacted by strong direct pressure, which could cause local extinctions of populations. Instead, *H. lucorum* populations in anthropogenic landscapes are usually dense and apparently well adapted. Morphometric studies were carried out on 12 populations from both anthropogenic and more natural habitats in a wide range of altitudes and climatic regimes in Georgia to investigate the effects of human pressure. Populations in more anthropogenic habitats have smaller adult shells independently of any effects of climate, altitude, or density. *H. lucorum* appears to adapt to anthropogenic pressures by changes in population dynamics, ceasing growth at a smaller size.

Key words: *Helix lucorum*, shell, size, adaptation, plasticity, Georgia

1. Introduction

Helix lucorum Linnaeus, 1758 is an abundant snail with a Mediterranean distribution. It is an edible snail, well adapted to human-modified landscapes such as gardens, parks, and arable land. In Georgia, *H. lucorum* is widely distributed and mostly found within or near settlements and in agricultural territory, while in natural habitats it is not very common – to date, only a few populations are documented in natural habitats, mainly in limestone areas of Georgia (Lejava, 1973; author's observation). This abundance in anthropogenic habitats is despite the heavy pressures associated with these habitats. In the lowlands of Georgia where intensive agriculture is developed (mainly winery, market gardening, and apple orchards), snails are considered one of the worst pests. Gardeners and villagers collect *H. lucorum* and burn or crush them several times per year (such influences are considered as a direct human impact throughout the text). In the cities, *H. lucorum* is mostly subject to accidental mechanical destruction and various other anthropogenic influences, such as pollution and habitat degradation. Clearly, there must be considerable differences in the dynamics of *H. lucorum* populations between anthropogenic and more natural habitats. Surprisingly, there is no research on the mechanisms involved in the survival and distribution of *H. lucorum* under such anthropogenic influence.

It is known that adult shell size and shape vary among populations of the same species of snail. There are marked responses in shell features to variation in environmental conditions, such as intraspecific competition, predation, parasitism, and environmental influence (for reviews see Goodfriend, 1986; Ożgo, 2008). High population density can restrict growth (Williamson et al., 1976; Cameron and Carter, 1979). This variation in shell characters undoubtedly has both hereditary and ecophenotypic components (Cook and Cain, 1980; Goodfriend, 1986; Baur, 1984, 1988), and it may have adaptive significance to local conditions (Chiba, 2009).

The present study explores whether shell characters of *H. lucorum* are correlated with anthropogenic disturbance. Considering edible snails (mainly *Helix* species) in general, Lubell (2004) suggested that the larger size of such species at prehistoric sites around the Mediterranean is a result of less disturbance and pollution than in modern times. We might hypothesize that if adult mortality is high, snails might mature at a younger age and smaller size. High densities might also limit growth. To test this idea, I compared shell sizes from 2 types of habitats, the first being undisturbed natural and anthropogenic habitat (NAH hereafter) where there is no extensive pressure by humans, and the other being anthropogenic habitat (AH hereafter) with extensive pressure.

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2. Materials and methods

2.1. Data collection and measurements

I collected samples of adult *H. lucorum* from NAH and AH sites during 2011 and 2012 (Figure 1, Table 1.). Brief descriptions of each site are as follows:

Pop1: Botanical garden, southwest outskirts of Tbilisi. Leghvtakhevi River ravine with polydominant forest and rocky slopes.

Pop2: 1 km west from Daba village with undisturbed alder forest.

Pop3: East outskirts of Katskhi village. Hornbeam (*Carpinus caucasica*) and beech (*Fagus orientalis*) mixed forest with limestone rocks. Very little grazing.

Pop4: Ateni village. Yard of Ateni church with old orchard. No disturbance.

Pop5: 2 km east from Sakramulo village. Dry hornbeam forest with limestone. Very little grazing or no disturbance.

Pop6: 600 m east from Igoeti village. Artificial mixed forest of 70–80 years old near the main road. Little or no disturbance.

Pop7: Tbilisi; parts of former garden with intensive littering and building.

Pop8: Outskirts of Tbilisi. Orchards. Owners of gardens collect snails every year and kill them.

Pop9: 1.5 km south of Broliskedi village. Forest of *Zelkova* (*Zelkova carpinifolia*) with limestone. Very intensive grazing.

Pop10: Tbilisi; Vakisparki garden. Artificial poplar (*Populus* sp.) trees. Very abundant population with very intensive physical destruction by humans.

Pop11: 700 m southwest of Aradeti village. Apple orchard. Villagers are physically destroying snails several times per year.

Pop12: Borjomi. City center, around the railway line. Various factors resulting in mechanical destruction.

In order to objectively assess shell size measurements, a strict definition of adult status was needed, but there are no earlier studies on this issue specifically for *H. lucorum*. However, Pollard (1973) regarded *H. pomatia* as fully adult when the lip of the aperture is reflected, after which it becomes thicker, with only a tiny increase in overall diameter. Based on this knowledge, only live snails with reflected lips were sampled at each point. In the laboratory 4 shell characters – shell height (SH), shell width (SW), aperture height (AH), and aperture width (AW) – were measured (Figure 2) using digital Vernier calipers with 0.05 precision. Two new variables expressing shell overall size (SOS) and aperture overall size (AOS) were derived by summing absolute height and width for shell and aperture, respectively.

2.2. Statistical analysis

For practical reasons, populations were selected for sampling only if density was sufficient to obtain an adequate number of adults within a 10 × 10 m plot. To investigate any density effect on shell sizes, I estimated densities using the following method: within each site where snails were found, each plot was divided into numbered subplots of 1 m². Three of these were selected at random at each site, and the number of adults found in each was used to estimate density per square meter (Table 1). Mean annual temperature and humidity values were extracted for each sampling point using ArcGIS 9.3. Climatic data were downloaded from http://worldclim.org (Hijmans et al., 2005).

Pearson's correlation was used to estimate the relationship between density and mean shell characters, and correlation analyses were also used to explore the influence of climate on shell size.

One-way ANOVA (with Tukey's post hoc test for multiple comparisons) was used to test the variation in
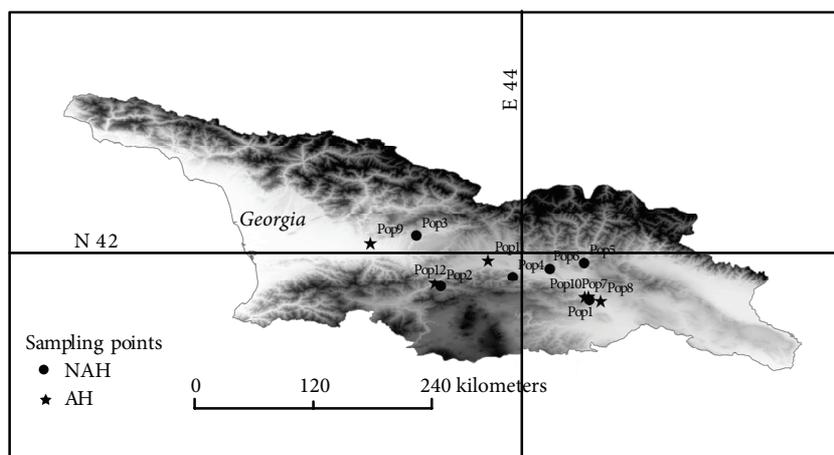

Figure 1. Map of the sampling localities in Georgia.

Table 1. Summary table of the collected data. Coordinates of sampling localities, altitude, mean density, number of sampled individuals, and the mean values (mm) of measured variables (with standard error of the mean) are shown.

Group	Pop ID	Coordinates	Altitude	Mean density	Measured individuals	Mean SH	Mean AH	Mean SW	Mean AW	Mean SOS	Mean AOS
NAH	Pop1	N41.684110 E044.792231	553	3.33	37	42.6 (0.4)	27.3 (0.2)	43.2 (0.3)	24.2 (0.2)	85.8 (0.7)	51.5 (0.4)
	Pop2	N41.811820 E043.438890	966	7.67	33	44.7 (0.3)	28.6 (0.4)	46.4 (0.3)	26.2 (0.2)	91.1 (0.7)	54.8 (0.6)
	Pop3	N42.284732 E043.217104	629	3.33	21	42.2 (0.6)	28.1 (0.4)	46.1 (0.6)	26.6 (0.2)	88.2 (1.2)	54.7 (0.7)
	Pop4	N41.904453 E044.094441	746	1.67	24	41.3 (0.3)	26.9 (0.2)	42.6 (0.3)	24.2 (0.2)	83.9 (0.7)	51 (0.5)
	Pop5	N42.034424 E044.744869	653	7.33	38	41.1 (0.2)	25.8 (0.1)	42.7 (0.2)	24.2 (0.1)	83.7 (0.5)	49.9 (0.3)
	Pop6	N41.979957 E 44.432056	711	9.67		44 (0.3)	27.9 (0.1)	44.5 (0.2)	25.6 (0.1)	88.4 (0.5)	53.5 (0.3)
AH	Pop7	N41.716093 E044.784564	433	7	29	38.5 (0.3)	24.6 (0.2)	39.7 (0.3)	22.7 (0.2)	78.2 (0.7)	47.2 (0.4)
	Pop8	N41.676460 E044.893970	426	7.33	23	38.3 (0.4)	25.3 (0.3)	40.5 (0.5)	23.2 (0.2)	78.7 (1)	48.5 (0.6)
	Pop9	N42.215146 E042.798710	130	2.33	31	35.8 (0.5)	23.8 (0.3)	39.5 (0.4)	23.2 (0.2)	75.2 (1)	47 (0.6)
	Pop10	N41.711319 E044.749842	488	6.67	51	36.7 (0.2)	23.2 (0.1)	38 (0.3)	22.3 (0.1)	74.6 (0.5)	45.4 (0.3)
	Pop11	N42.057500 E043.869400	676	3.67	35	36 (0.3)	23.3 (0.2)	38.1 (0.3)	21.6 (0.3)	74.1 (0.8)	44.8 (0.5)
	Pop12	N41.841969 E43.385347	794	10.33	36	38.2 (0.2)	24 (0.1)	40.1 (0.2)	23.3 (0.1)	78.2 (0.5)	47.2 (0.3)

size measurements between and within groups (NAH and AH) (Sokal and Rohlf, 1995). Principle component analysis (PCA) based on the correlation matrix (Joliffe and Morgan, 1992) was used to visualize shell size differences between populations using 4 empirical measurements.
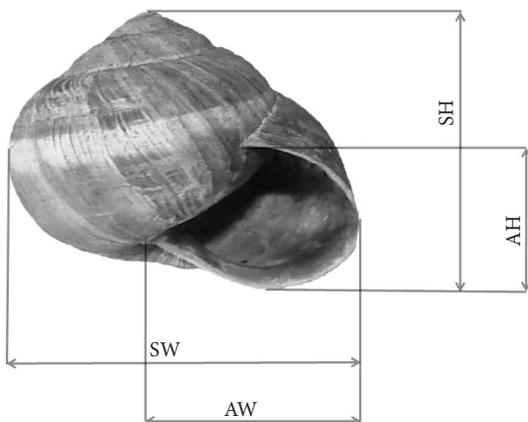

Figure 2. Measurements of the shells of *Helix lucorum* used in the analysis: SH, shell height; SW, shell width; AH, aperture height; AW, aperture width.

For data handling and correlation analysis, a spreadsheet (Microsoft Excel) was used. ANOVA and PCA were performed in SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

3. Results

In total, 412 adult individuals (207 from 6 NAH and 205 from 6 AH populations) were collected and measured (Table 1). Sampling sites are distributed within an altitude range from 130 m to 966 m above sea level (Figure 1). Pearson's r statistics showed no significant correlations between measured shell characters and population densities, altitude, mean annual temperature, or mean annual humidity (for all combinations $P > 0.05$).

After ANOVA, every NAH population had a significantly higher mean overall size (SOS) than AH populations (Tukey's HSD post hoc test), whereas populations within each of the groups showed no significant differences (Table 2, Figure 3). Almost identical results were derived for the AOS variable except one: Pop5 does not have a significantly higher mean apertural overall size than Pop8.

The PCA extracted 2 components with eigenvalues exceeding unity. The first PC explains 89% of total variation

Table 2. Results of Tukey's multiple tests after ANOVA. Bold-italic font denotes significant results. Positive values above the diagonal indicate that the population on the left of the chart (column 1) has a higher mean value compared to respective population at the top of the table (row 1), and vice versa for values below the diagonal. Highlighted values show that overall size for shell and aperture is consistently higher in NAH populations.

	Pop1	Pop2	Pop3	Pop4	Pop5	Pop6	Pop7	Pop8	Pop9	Pop10	Pop11	Pop12
Pop1	0	*-0.33*	*-0.33*	0.05	0.15	*-0.2*	*0.42*	*0.3*	*0.45*	*0.61*	*0.66*	*0.43*
Pop2	*-0.06*	0	0.01	*0.38*	*0.48*	0.13	*0.75*	*0.63*	*0.78*	*0.94*	*1*	*0.76*
Pop3	-0.03	0.03	0	*0.37*	*0.48*	0.13	*0.75*	*0.63*	*0.77*	*0.93*	*0.99*	*0.76*
Pop4	0.02	*0.08*	0.05	0	0.11	*-0.24*	*0.38*	*0.26*	*0.4*	*0.56*	*0.62*	*0.39*
Pop5	0.02	*0.08*	*0.05*	0.01	0	-0.35	*0.27*	0.15	*0.29*	*0.46*	*0.51*	*0.28*
Pop6	-0.03	0.03	-0.01	*-0.05*	*-0.06*	0	*0.62*	*0.5*	*0.65*	*0.81*	*0.86*	*0.63*
Pop7	*0.09*	*0.15*	*0.12*	*0.07*	*0.07*	*0.12*	0	-0.12	0.02	0.19	*0.24*	0.01
Pop8	*0.09*	*0.15*	*0.11*	*0.07*	*0.06*	*0.12*	-0.01	0	0.15	*0.31*	*0.36*	0.13
Pop9	*0.13*	*0.19*	*0.16*	*0.11*	*0.11*	*0.16*	0.04	0.05	0	0.16	*0.22*	-0.02
Pop10	*0.14*	*0.2*	*0.17*	*0.12*	*0.12*	*0.17*	*0.05*	*0.05*	0.01	0	0.06	-0.18
Pop11	*0.15*	*0.21*	*0.18*	*0.13*	*0.12*	*0.18*	*0.06*	*0.06*	0.02	0.01	0	*-0.23*
Pop12	*0.09*	*0.15*	*0.12*	*0.07*	*0.07*	*0.12*	-0.01	0.01	-0.04	*-0.05*	*-0.06*	0

Above the diagonal: **AOS**, $F_{11,400} = 65.03$, $P < 0.0001$; Below the diagonal: **SOS**, $F_{11,400} = 73.17.03$, $P < 0.0001$.

where all 4 measured variables have high positive loadings and the ratios have small negative loadings. In contrast, the second PC explains 6% of total variations, and neither of the variables have high positive or negative loadings (Table 3). A result of ANOVA and PCA suggests that increasing any one dimension of the shell also increases the other. The differences between NAH and AH populations along the first and second PC are shown in Figure 4.

4. Discussion

Variations in shell size and form in helicoid snails have been extensively investigated and mechanisms underlying this variation are attributed to combinations of various environmental factors, inter- or intraspecific interactions, and genetic processes (Goodfriend, 1986). However, there are no data on how *H. lucorum* responds in shell size to external factors or on the heritability of shell size
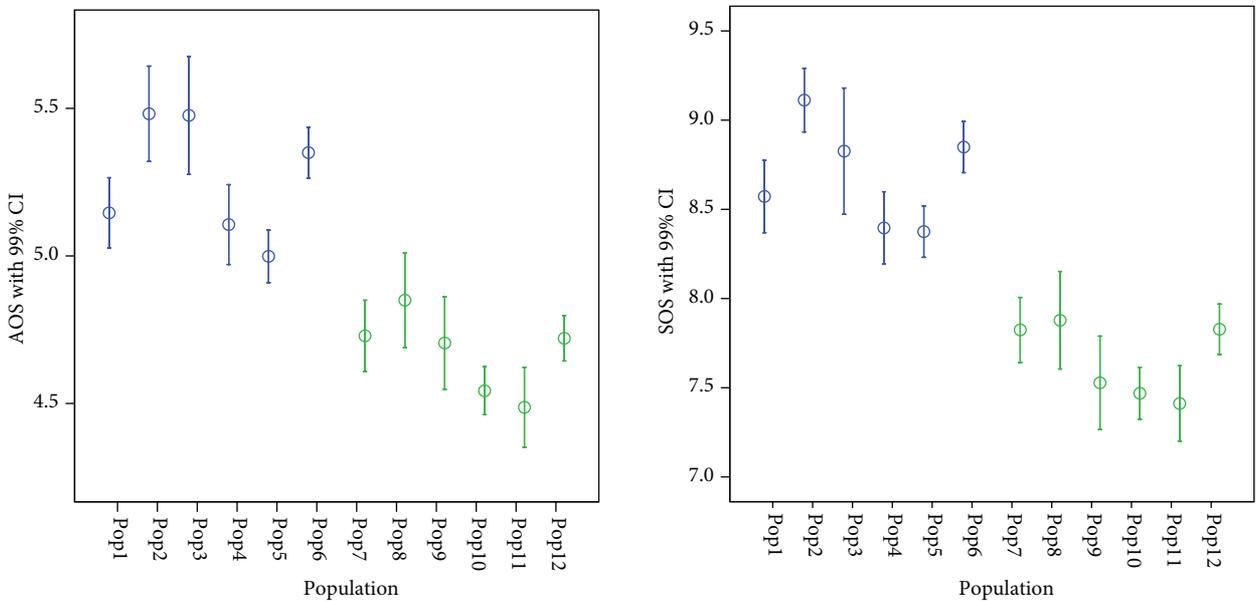

Figure 3. Error bars of mean values of SOS and AOS variables are shown with 99% confidence intervals.

Table 3. PCA loadings are shown for PC with eigenvalues exceeding unity.

Variable	PC1	PC2
SH	0.935	−0.293
AH	0.954	−0.120
SW	0.979	0.042
AW	0.920	0.377

differences. Only a few published papers are available concerning the life cycle, genital anatomy, growth, reproduction, and activity of *H. lucorum* (Lazaridou-Dimitriadou and Saunders, 1985; Staikou et al., 1987; Lazaridou-Dimitriadou and Bailey, 1991; Osselaer and Tursch, 2000).

The results shown here indicate that shell size in *H. lucorum* is influenced by factors associated with human activity, to the extent that other potentially important factors such as climate and population density appear irrelevant. I have no means at present to determine the extent to which this influence is direct and ecophenotypic or the result of hereditary adaptation to the prevailing conditions. Work on other species suggests that this balance may vary among species and circumstances (Goodfriend, 1986; Baur, 1988). In many studies, large adult size is correlated with rapid growth (Williamson et al., 1976; Baur, 1984; Gould, 1984; Goodfriend, 1986), but we have yet to establish this connection in *H. lucorum*. The lack of any direct relationship between size and density is particularly noteworthy, as this has been reported in many species (Goodfriend, 1986), and, in general, AH habitats support higher densities than NAH in Georgia. A greater range of densities might demonstrate a link.

Whatever the causes, these results show a form of adaptability in *H. lucorum* populations of a kind not yet reported in other snails. We can hypothesize that high adult mortality may put a premium on early maturity and reproduction where potentially long-lived adults have less chance of surviving from year to year. Alternatively, in populations where direct human impact (i.e. collecting and killing snails) is very strong, snails are smaller in size because it is easier for them to hide effectively. In this context, humans can be considered as predators; Bantock and Bayley (1973) demonstrated that predators
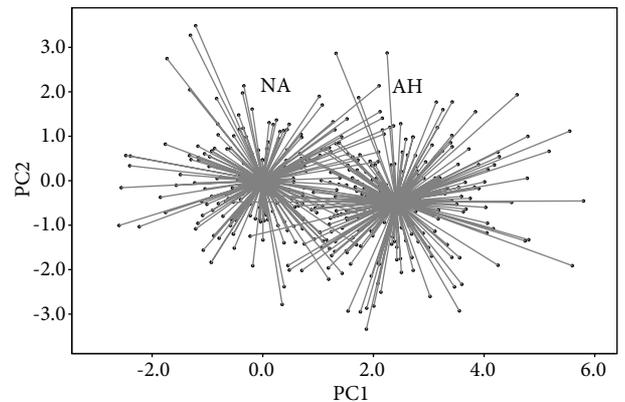

Figure 4. Individual scores of the *Helix lucorum* along the first 2 PCA axes defined by size variables and 2 ratios.

selected larger individuals in *Cepaea* populations. Changes or differences in shell morphology as a result of adaptations are well known for other snails (Konuma and Chiba, 2007; Chiba, 2009). However, populations in anthropogenically heavily impacted habitats (e.g., big cities where snails are not considered pests and hence are not collected deliberately to be killed) are revealing similar size distribution to the populations under direct human impact in contrast to natural ones.

Certainly, this study provides no evidence that some factors influential in other species, for example crowding or interspecific competition (Williamson et al., 1976; Baur, 1988), are strong enough to override the effects of human activity. *H. lucorum* is a widespread species, undoubtedly spread by humans, originally for food (Lubell, 2004). Responses to pressures of this kind are likely to be common to most populations, rather than a consequence of specific adaptations evolved independently in each. More research, perhaps especially on the population dynamics and growth patterns of *H. lucorum* and other large, edible helicids, might shed light on the specific factors involved.

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