Environmental influence on shell characters in alpine Arianta arbustorum (Gastropoda: Helicidae)

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Environmental influence on shell characters in alpine *Arianta arbustorum* (Gastropoda: Helicidae)

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ABSTRACT Contrib. Nat. Hist. 6: 1–13.

Populations of the land snail *Arianta arbustorum* (L.) from different mountain peaks in the Swiss Alps were investigated biometrically. The study sites were situated between 2150 and 2660 m above sea level. Shell characters were influenced by altitude and orientation of the slope. Shell size diminished with increasing altitude, which is obviously a general feature of the species. In populations with a southern orientation, shells became darker with increasing altitude. It is suggested that, at very high altitudes, a dark shell colour allows the snails to warm up faster when activity time is critically short, and also protects from ultraviolet radiation. Body colour was affected neither by altitude nor by orientation of the slope.

Keywords: Gastropoda, Helicidae, *Arianta arbustorum*, mountain peaks, Swiss Alps, shell size, shell colour, body colour.

Introduction

The European land snail *Arianta arbustorum* (Linnaeus, 1758) shows high phenotypic variability that is related both to habitat and to altitude (Burla & Stahel 1983, Gittenberger 1991). Variation is continuous between large brown morphs, occurring mainly in forests at low altitudes, and small yellow morphs in grassland at higher altitudes. However, colour polymorphism still occurs at high altitudes, though noticeably shifted to pale hues. In Switzerland, *A. arbustorum* is found from the lowland to mountain peaks in the Alps, covering a vertical range of about 2500 metres. The most elevated populations are known from the Grisons in the eastern part of Switzerland: Val Ftur, 2640 m, and Val dal Botsch, 2660 m, in the Lower Engadine (Bütikofer 1920) and Piz Martegnas, 2670 m (Burla & Stahel 1983). Snails at high altitudes have to cope

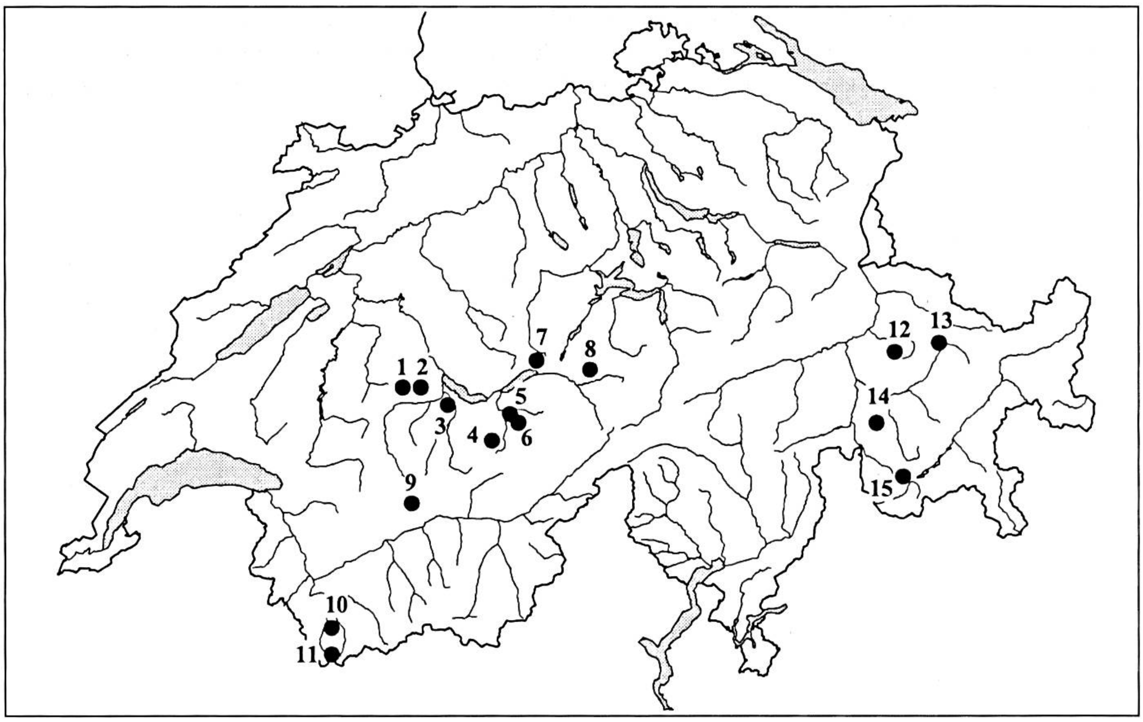


Fig. 1. Sites in the Swiss Alps where populations of *Arianta arbustorum* were studied. The population numbers match those in Table 1 and Table 2.

with extreme environmental conditions such as short summers, intense solar radiation, low humidity, and temperatures below zero even in midsummer. As a response to harsh environment, alpine *A. arbustorum* were selected for solar radiation resistance (Burla & Gosteli 1993), and special life-history traits have evolved (Baur & Raboud 1988). Studies dealing with altitudinal variation in *A. arbustorum* showed a special pattern in shell colour (Burla & Stahel 1983, Baur & Raboud 1988): Shells become paler with increasing altitude and are palest at about 2000 m. At altitudes above 2000 m dark phenotypes may show up again. The question is if this trend towards melanism, found within a single slope, is generally valid and can also be observed, when separate populations are compared. The present study biometrically compares populations of *A. arbustorum* from different mountain peaks in the Swiss Alps, where the species is at the very extreme of its range, and reports on influence of altitude and orientation of the slope on shell and body characters.

Material and methods

Between 1995 and 2001 live adult *A. arbustorum* were collected at 15 different localities in the Swiss Alps (Fig. 1). The collecting sites were situated on or near mountain peaks between 2150 and 2660 m above sea level (Table 1). Usually, only small populations of *A. arbustorum* could be found at peak sites. The

Table 1. Localities in the Swiss Alps, where populations of *Arianta arbustorum* were investigated, with altitude (Alt, in metres above sea level), orientation (Orient, in degrees; asterisks indicate populations with southern orientations), angle of inclination (Incl, in degrees), and numbers of investigated live snails (N).

No	Locality	Alt	Orient	Incl	N
1	Gantrisch BE	2150	0	10	27
2	Stockhorn BE	2165	*180	40	14
3	Niesen BE	2355	123	42	20
4	Birg (Mürren) BE	2550	*194	30	25
5	Männlichen BE	2330	90	35	23
6	Lauberhorn BE	2465	70	36	20
7	Brienzer Rothorn BE	2300	*199	30	25
8	Balmeregghorn BE	2225	*145	10	25
9	Bella Lui VS	2520	92	30	20
10	Tour de Bavon VS	2400	*180	30	20
11	Clocher de la Chaux VS	2460	240	40	10
12	Weisshorn (Arosa) GR	2610	*175	38	15
13	Schiahorn GR	2650	*187	30	17
14	Piz Martegnas GR	2660	130	30	21
15	Motta da Sett GR	2510	50	30	20

snails were often continuously distributed over a large area. However, neighbourhood area in *A. arbustorum* corresponds to a circle with a diameter of 32 to 50 m (Baur 1993), which means that individuals hatched more than 50 m apart are isolated and belong to different subpopulations. For that reason all investigated populations were collected within a diameter of 50 m. Usually, about half a metre was paced off between collected snails to avoid sibling sampling. The samples were taken in alpine meadows that were often interspersed with boulders. Some of these localities are disturbed by tourists. The resident snail populations are obviously not endangered, because they normally dwell in steep and inaccessible sites remote from tourist paths. The snails were scored for five characters (Table 2). For colouring characters arbitrary categories were used. The snails were compared with hand made colour scales, one special scale for each character. Shell colour: seven classes from pale yellow (1) to dark brown (7); body colour: photographs of different snails from pale (1) to dark (5); density of white flecks on the shell: photographs of different shells from unflecked (1) to totally flecked (7). In all, 302 live snails were measured and then released on the spot. Data analysis was performed using the SPSS 9.0 program package (SPSS Inc. Chicago, 1999). Shell volume was calculated according to the formula given by Rensch (1932): Shell volume $= (\text{width})^2 \times \text{height}/2$.

Table 2. Shell characters and body colour of adult *Arianta arbustorum* from different mountain peaks. Numbers of localities as in Table 1. Values are means ± S.D. Lengths are in millimetres. Shell colour is coded in seven classes from pale yellow (1) to dark brown (7), density of white flecks on the shell is coded in seven classes from unflecked (1) to totally flecked (7), and body colour ranges from pale (1) to dark (5). N = number of snails analysed per population.

Loc	N	Height	Width	Shell colour	Flecking	Body colour
1	27	13.44 ± 0.94	16.24 ± 0.76	4.9 ± 1.5	4.2 ± 1.2	3.1 ± 1.0
2	14	14.10 ± 0.93	17.47 ± 0.76	2.0 ± 0.6	6.5 ± 0.5	3.1 ± 0.9
3	20	14.34 ± 0.73	17.62 ± 0.52	2.6 ± 0.7	5.5 ± 1.3	2.4 ± 0.7
4	25	9.64 ± 0.47	11.97 ± 0.47	3.0 ± 0.8	4.9 ± 1.1	2.2 ± 0.7
5	23	13.43 ± 0.61	16.79 ± 0.49	3.7 ± 0.6	5.0 ± 1.2	2.9 ± 0.9
6	20	12.93 ± 0.64	15.75 ± 0.50	4.1 ± 1.1	4.8 ± 1.2	2.2 ± 0.7
7	25	13.45 ± 0.69	16.53 ± 0.72	2.4 ± 0.8	5.8 ± 1.1	2.1 ± 0.7
8	25	13.61 ± 0.89	17.23 ± 0.69	2.2 ± 0.8	5.6 ± 1.0	2.0 ± 0.3
9	20	11.95 ± 0.67	15.31 ± 0.86	3.0 ± 0.8	5.7 ± 0.5	2.7 ± 0.7
10	20	13.74 ± 0.70	17.67 ± 0.78	2.9 ± 0.7	6.6 ± 0.5	2.9 ± 0.7
11	10	12.60 ± 0.38	16.03 ± 0.68	2.5 ± 1.0	6.7 ± 0.5	2.5 ± 0.5
12	15	12.83 ± 0.90	15.16 ± 0.55	3.5 ± 0.5	4.8 ± 0.9	2.2 ± 0.8
13	17	10.37 ± 0.74	12.92 ± 0.78	3.9 ± 1.3	5.2 ± 1.0	2.9 ± 1.0
14	21	12.37 ± 0.76	15.07 ± 0.92	2.9 ± 0.8	5.6 ± 1.1	3.4 ± 1.0
15	20	14.46 ± 0.76	17.73 ± 0.80	5.4 ± 0.9	4.6 ± 1.1	2.8 ± 0.8

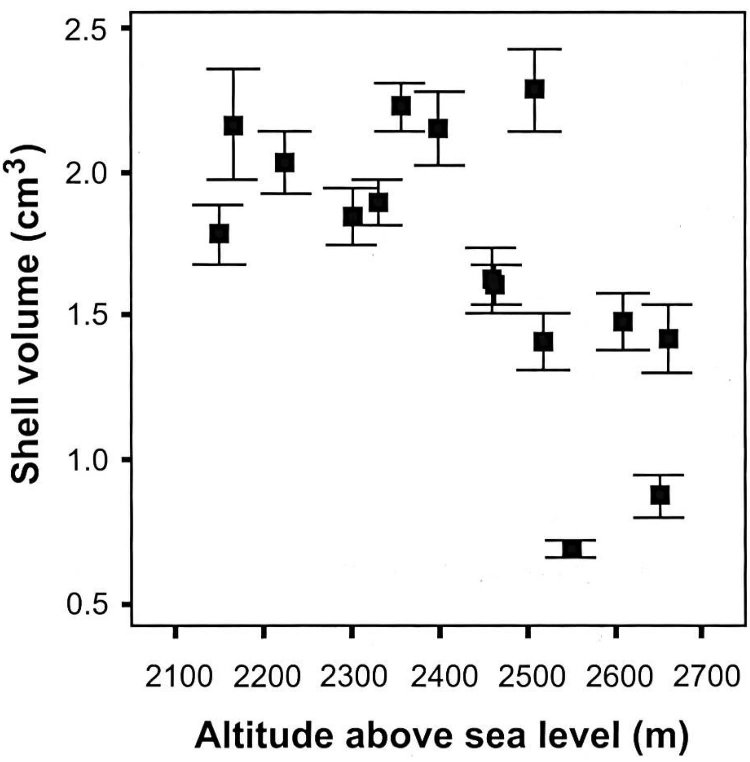


Fig. 2. Mean shell volume (with 95 % confidence interval) in *Arianta arbustorum* in relation to altitude.

Results

Shell size decreased with increasing altitude (Fig. 2). In terms of shell volume, the smallest snails from very high altitudes were less than half the size of their conspecifics from lower sites. Some of the investigated populations did not follow the general trend. The smallest shells were not from the most elevated site (Piz Martegnas, 2660 m, population No. 14) but came from Birg (Mürren) at 2550 m (population No. 4), with means of 9.64 mm for shell height and 11.97 mm for shell width respectively (Table 2). The largest means in shell size were recorded in population No. 15 from Motta da Sett at 2510 m (shell height: 14.46 mm, shell width: 17.73 mm). This could be due to special topographic conditions. The Birg population, living on a rounded hilltop, is extremely exposed, while the snails from Motta da Sett live well protected in a hollow with an easterly aspect. To give an idea of how small alpine *A. arbustorum* can be, 19 snails from lowland populations around Zurich (400–500 m above sea level) were measured for comparison. The means for shell height and width are 16.8 mm and 22.7 mm respectively. In Plate 1 shells from Birg, Motta da Sett and Zurich are compared.

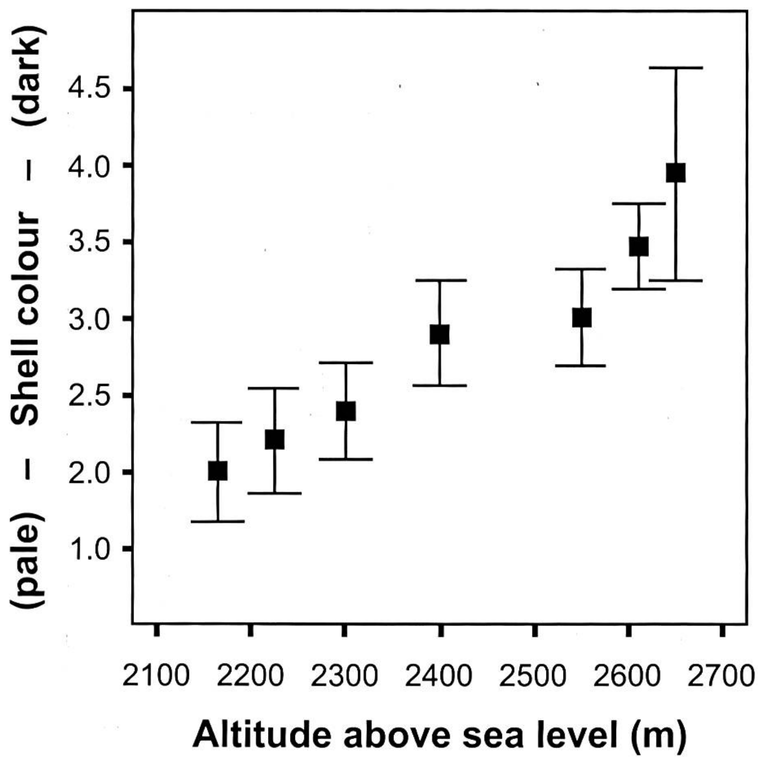


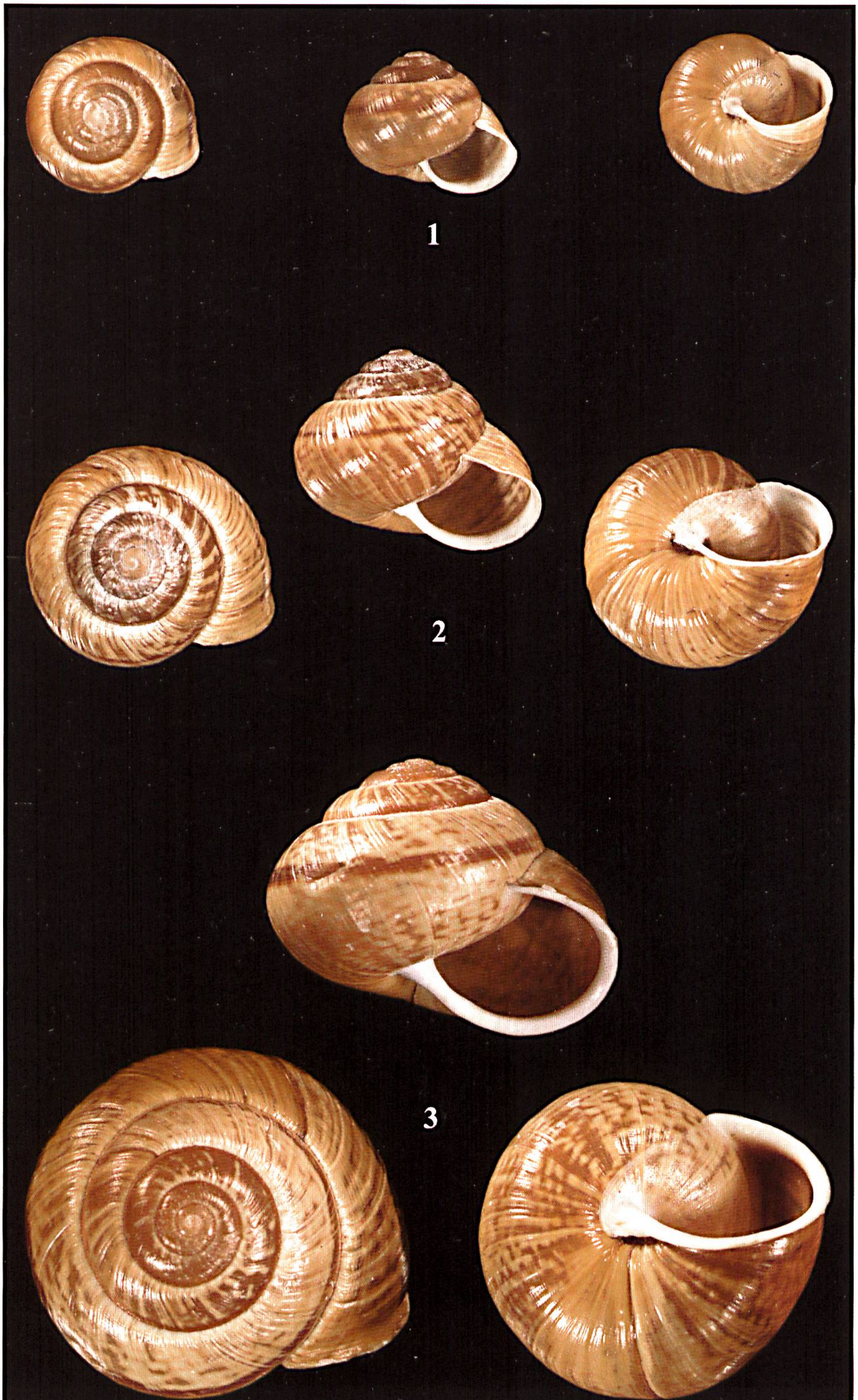
Fig. 3. Mean shell colour (with 95% confidence interval) in *Arianta arbustorum* in relation to altitude. Only snails of populations with southern orientations are considered (SE to SW): Stockhorn (2165 m), Balmeregghorn (2225 m), Brienzer Rothorn (2300 m), Tour de Bavon (2400 m), Birg (2550 m), Weisshorn (2610 m), Schiahorn (2650 m).

Table 3. Pairwise comparisons of shell colour from different altitudes (Alt) by Mann-Whitney U-Test. Values indicate the probability of error that colours are different.

Alt	2650	2610	2550	2400	2300	2225	2165
2650	–						
2610	0.295	–					
2550	0.012	0.051	–				
2400	0.007	0.019	0.547	–			
2300	0.000	0.000	0.006	0.032	–		
2225	0.000	0.000	0.001	0.007	0.425	–	
2165	0.000	0.000	0.000	0.001	0.097	0.419	–

If only populations with a southern orientation were considered (angle of orientation: SE 140° to SW 220°), shells became darker with increasing altitude (Fig. 3, Table 3). Each population consisted of individuals with continuously varying shell and body colours (Fig. 4). The two colour features varied independently except in the populations from Birg (2550 m) and Schiahorn (2650 m), where shell and body colours were positively correlated (Spearman correlation, $p < 0.05$ in both populations). Body colour showed no correlation with altitude. The density of light flecking of the shell diminished with altitude but not in a linear manner (Fig. 5). No correlations of shell and body colour with altitude could be found in populations with eastern orientations.

Plate 1. *Arianta arbustorum* from three different localities in Switzerland. (1) Birg, Mürren, 2550 m above sea level, (2) Motta da Sett, 2510 m, (3) Zurich, 400 m. All figures scaled 2x.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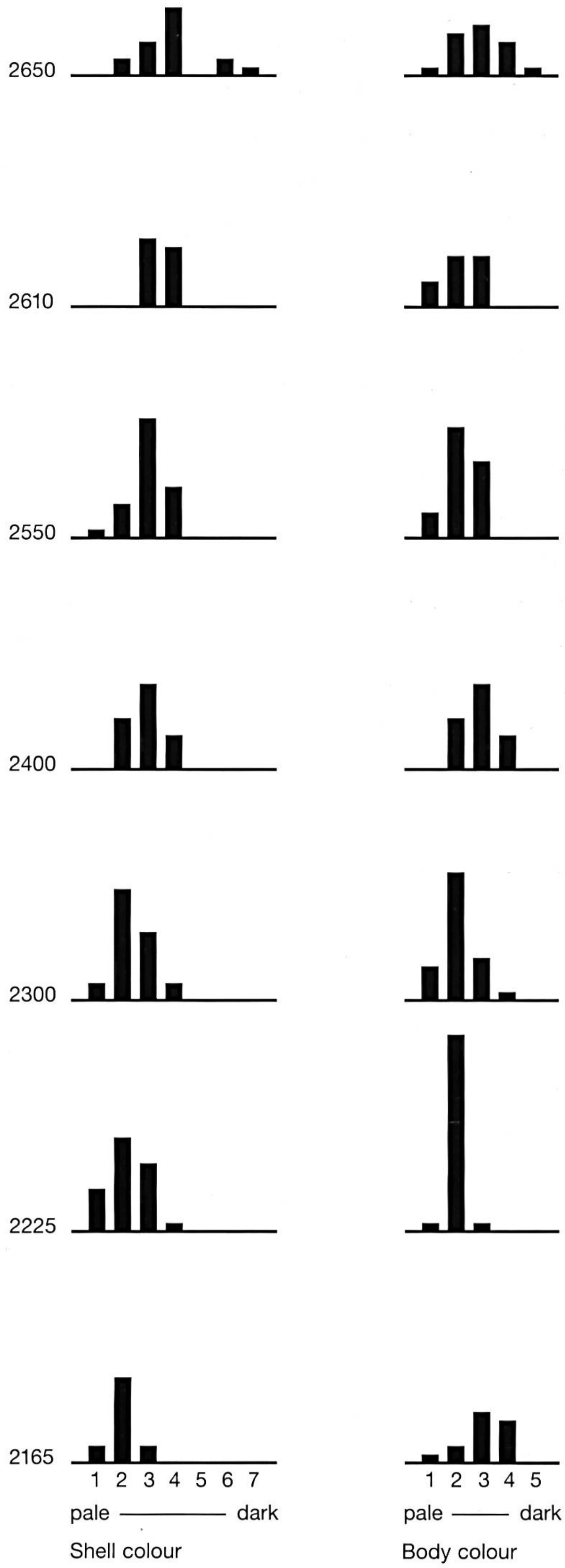

Fig. 4. Frequency distributions of darkness of shell colour (7 classes) and darkness of body colour (5 classes) in *A. arbustorum* from south-oriented populations, altitude indicated at left. Sample size as in Table 1.

Discussion

The finding that shell size in *A. arbustorum* diminishes with increasing altitude confirms previous studies (Burla & Stahel 1983, and references therein, Baur 1984, Baur & Raboud 1988). However, the cited studies compared snails from a transect line of a single slope, whereas in the present case snails from separate mountain peaks are compared. The general decrease in shell size with increasing altitude has to be attributed to stressful environment at alpine sites caused by harsh climate. However, small shells at high altitudes are not only environmentally induced but also have a genetic basis (Baur 1984). Population density, which is known to affect shell size negatively (Goodfriend 1986), is probably not a stress factor for *A. arbustorum* on mountain peaks. In most of the investigated populations density was rather low.

Climate at alpine sites is influenced not by altitude alone but also by the angle and the orientation of the slope (Franz 1979, Barry 1992). Sites with a southern aspect are subject to rapid changes in temperature, humidity, and snow cover due to high insolation. Compared to other orientations north-facing slopes are coldest. In the present study only the Gantrisch population faced northwards, but the site had a weak inclination of only 10 degrees and was the lowest of all investigated sites. No *A. arbustorum* were found on more elevated

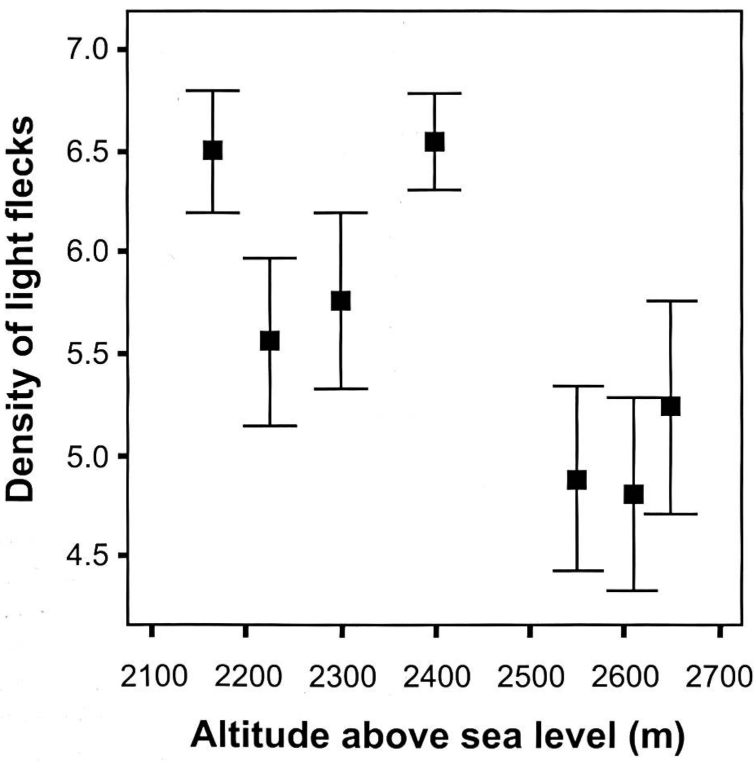

Fig. 5. Mean density of light flecks on the shell of *Arianta arbustorum* (with 95% confidence interval) in relation to altitude. Only populations with southern orientations are considered.

northern slopes. Arter (1990), who investigated snails along an 8-km contour line at an elevation of 2000 m on Piz Martegnas, found bigger shells and heavier bodies on east-facing slopes than on north- and south-facing slopes.

Temperature at the soil surface depends on both solar radiation and soil humidity. At night, plant cover becomes wet with dew. In the morning humidity evaporates, keeping the temperature at a low level. In the afternoon, the temperature increases rapidly because there is no humidity to balance it. That is why south-west-facing slopes are especially warm and dry while south-east-facing slopes are relatively cold and humid (Franz 1979). This could explain why *A. arbustorum* is very rare on south-west-facing slopes. Almost no snails were found on western slopes either, which can perhaps be attributed to the influence of wind. West wind is common in the Swiss Alps, and snails exposed to it run the risk of desiccation.

Colours of shell and body of *A. arbustorum* are thought to vary rather with habitat than with altitude (Burla & Stahel 1983, Arter 1990). Dark-shelled animals normally occur in shaded places where colour has the function of camouflage (Parkin 1971). In open habitats such as alpine meadows, selection favours pale shells because they absorb less solar radiation and have a lower risk of overheating (Burla & Gosteli 1993). At altitudes higher than 2000 m shells become darker again. There, the function of dark colour is not that of camouflage but of a more rapid warming up when activity time is critically short. A dark shell colour might also shield from ultraviolet radiation (Heller 1979, Burla & Stahel 1983), which is much stronger at high altitudes (Barry 1992) and can cause genetic damage. On south-facing slopes insolation is heaviest (Franz 1979), and a dark shell protecting from ultraviolet rays becomes more and more important with altitude. This would explain the linear increase of dark shell with increasing altitude, which could only be found in populations with southern orientations. Selection pressure towards dark shells is expected to be strong on east-facing slopes as well, because insolation there is only weak. Mean shell colour in all snails with eastern orientations (population number 3, 5, 6, 9, 14, and 15, Table 1) is indeed darker (= 3.6, in a scale ranging from 1 to 7) than in snails with southern orientations (= 2.8). Arter (1990) obtained similar results on Piz Martegnas, where shells from north-facing slopes were darkest. As these slopes also had a thick plant cover, Arter (1990) attributed the dark shell colour to visual selection, preventing predators from finding the snails within dense vegetation on a dark soil background. Associations between shell colour and local microclimate were also found in the helicid snail *Cepaea vindobonensis* (Honek 2003).

Two factors, ground colour and density of light flecking, determine shell colour of *A. arbustorum*. Ground colour varies from pale yellow to dark brown, light flecks can be absent or vary from a distinct pattern to a nearly closed cover. In pale shells ground colour and flecking can be of identical hue. Flecked areas are thicker than those without flecks (M. Gosteli, personal observation). Together with pale ground colour of the shell, light flecks may prevent the snails from overheating by reflecting solar radiation. While shell ground colour is shifted to dark hues at very high altitudes, light flecking diminishes. Both tendencies result in melanistic phenotypes. Melanism can be observed in various cold-adapted invertebrates (see for instance Sømme & Block 1991). As light flecks are often less pronounced in juvenile *A. arbustorum*, their shells appear darker than those of adults of the same population, as seen in the first whorls of the shells in Plate 1. Juveniles expose themselves more often to the sun than adults (M. Gosteli, personal observation). By speeding up temperature-dependent processes, a dark shell assists the young snail to mature rapidly and reach reproduction size faster (Heller & Volokita 1981).

Interestingly, body colour is not affected by altitude. In a crawling snail the fully extended soft body is a target for solar radiation. However, the daily distances covered by *A. arbustorum* are short (Baur 1993, Kleewein 1999), and the snails are active mainly at night or in the twilight. During sunny days, they keep still in a shelter, withdrawn into the shell. It is mainly the shell that is exposed to the sun. This is probably the reason why the colour of the shell and not that of the body is under selection.

On mountain peaks in the Alps the land snail *A. arbustorum* is at the species border. Most of the investigated populations are small. Abiotic stress seems to be the limiting factor. Organisms living at the very extremes of a species range are not the fittest members of their species (Parsons 1996). However, as Hoffmann & Blows (1994) pointed out, marginal populations do not necessarily suffer from poor conditions, but may be well adapted to their unfavourable environment. Alpine *A. arbustorum* seem to fit this suggestion, showing a special life-history pattern with a slow rate of development, late maturity, long lifespan and low fecundity (Baur & Raboud 1988). Additional adaptations such as melanism in shell colour and a greater freezing resistance (Stöver 1973) help the snails to survive adverse environmental conditions.

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