Articles

SNAILS ON THE ROCKS

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Abstract

A pilot study was carried out at three adjacent rock faces at a location in the Northern calcareous Alps (Johnsbach,Styria, Austria) to estimate population sizes, densities, activity range and small-scale distribution patterns of selected rock-dwelling snails. The study site was a about 15 m long rock face naturally divided into three parts. These three rock faces were subdivided into 10 sections each 1.5 m wide and 3 m high. Those were again subdivided by a grid of 50 × 50 cm cell size on printed photographs of the sections to facilitate recording of positions of snails. On two days (21.08.2017, 23.08.2017) between 10:00 – 11:30 a.m. each section was investigated by a team of three people. Each team used particular colors for marking the snails to enable recapture. Eight species of land snails were recorded, with *Pyramidula pusilla/ saxatilis* and *Chondrina avenacea* being the most abundant. Only sparse dispersal of snails from one section to another section was recorded. The re-capture rate was in general high, but could not be evaluated for species encountered in low frequencies only *(Cochlodina laminata, Chilostoma achates* and *Petasina unidendata*). For *Chondrina avenacea*, *Neostyriaca corynodes*, *Clausilia dubia* and *Orcula gularis* there was a high re-capture rate. Together with the observation that snails almost never crossed borders of sections, one can assume that these species were quite immobile at least at the timescale of the study. Concerning *Pyramidula pusilla/saxatilis*, the calculated values of population size/densities were

considerably higher than the counts. This can be explained by higher activity / mobility but might also be due to low visibility and finding probability. For *Pyramidula pusilla/saxatilis* there was a statistically significant deviation from uniform height distribution within the areas investigated. It was mostly absent below 50 cm above ground and most abundant in heights about 100 – 150 cm above ground.

Keywords: rock dwelling, terrestrial gastropods, population sites, microdistribution, dispersal

INTRODUCTION

While for many gastropods knowledge on biology, behaviour and ecology is minimal, such information would help to address questions of evolutionary processes and mechanisms like adaptation, selection and speciation. Some studies have addressed ecological questions on snails which partly occur on rocky habitats (e.g. Ledergerber et al. 1997; Bisenberger et al. 1999; Kleewein 1999; Baumgartner et al. 2000; Junker 2015; Junker 2016) and only a few studies particularly focused on typical rock-dwelling snails (e.g. Baur & Baur 1995; Giokas & Mylonas 2004; Schmera et al. 2015; Marković et al. 2018).

In general, details of life history, micro-habitat preferences, reproductive biology and food ecology of terrestrial snails are much in demand. In the course of the Alpine land snails workshop 2017 a pilot study was carried out at a rock face near Johnsbach (Styria, Austria). The aims were to determine occurrence of rock dwelling land snail species composition at this site as well as to estimate population sizes and densities and to get insights into activity range and small-scale distribution patterns. The study also includes a descriptive part as information on the rock face, e.g., variation in the texture, plant communities, as well as observation of other invertebrate animals, were recorded.

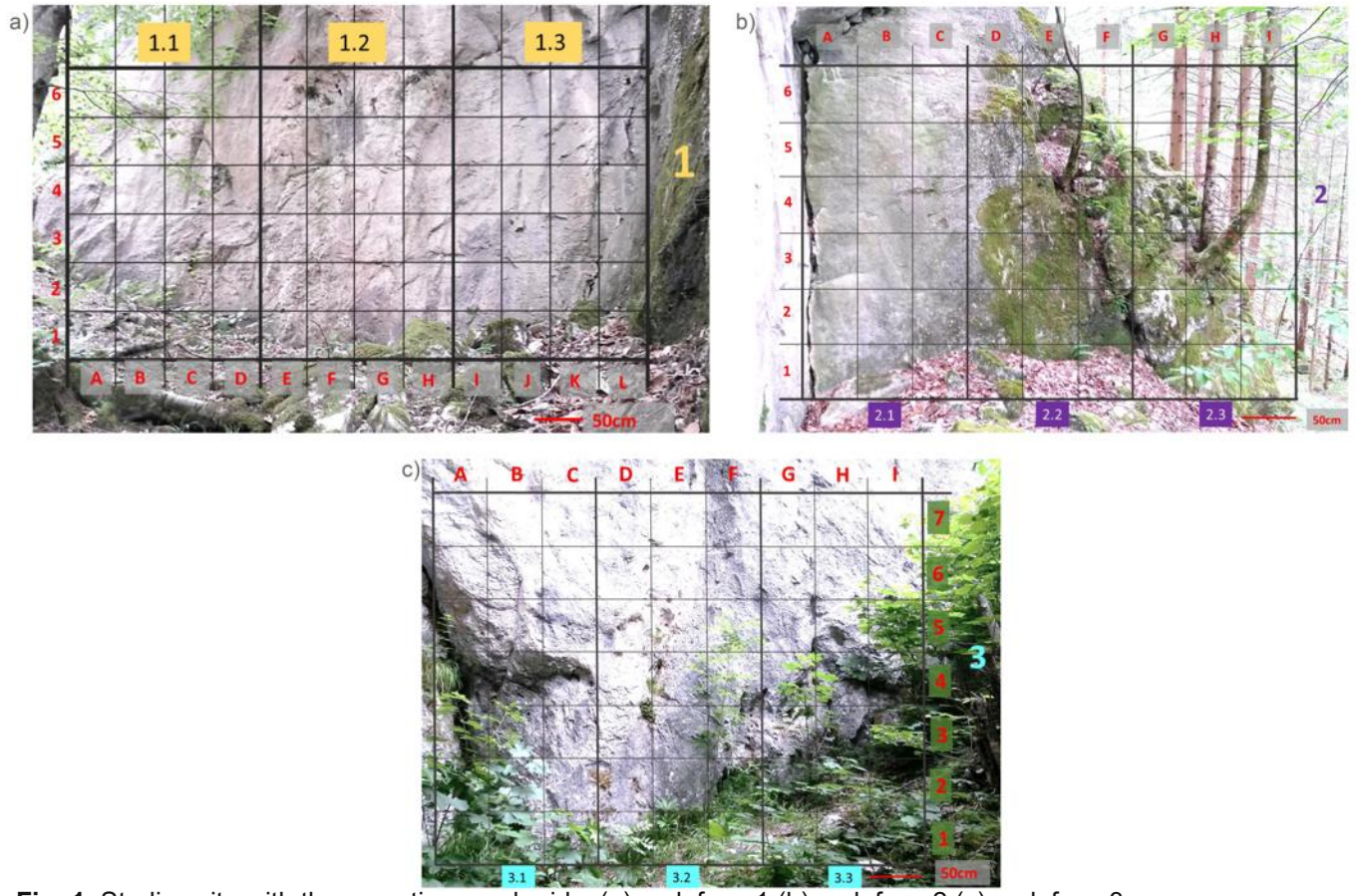

Fig. 1. Studies site with three sections and grids. (a) rock face 1 (b) rock face 2 (c) rock face 3

MATERIAL AND METHODS

Description of sampling site

The study site (at 47°32'17" N, 14°37'26" E) is a steep limestone rock face situated at the formation Wolfbauer Mauer, to the east of the Wolfbauer Wasserfall in Johnsbach (Styria, Austria). These calcareous rocks represent Middle Triassic Steinalm formation (Kreuss 2014). The study site is located in a montane spruce-fir-beech forest on limestone, which is the most frequent forest type in the National Park Gesäuse (Carli 2007). The exposition of the nearly vertical rock face is south to southwest. The altitude of the rock base is 1020 m asl, the height of the entire wall reaches approximately 80 m.

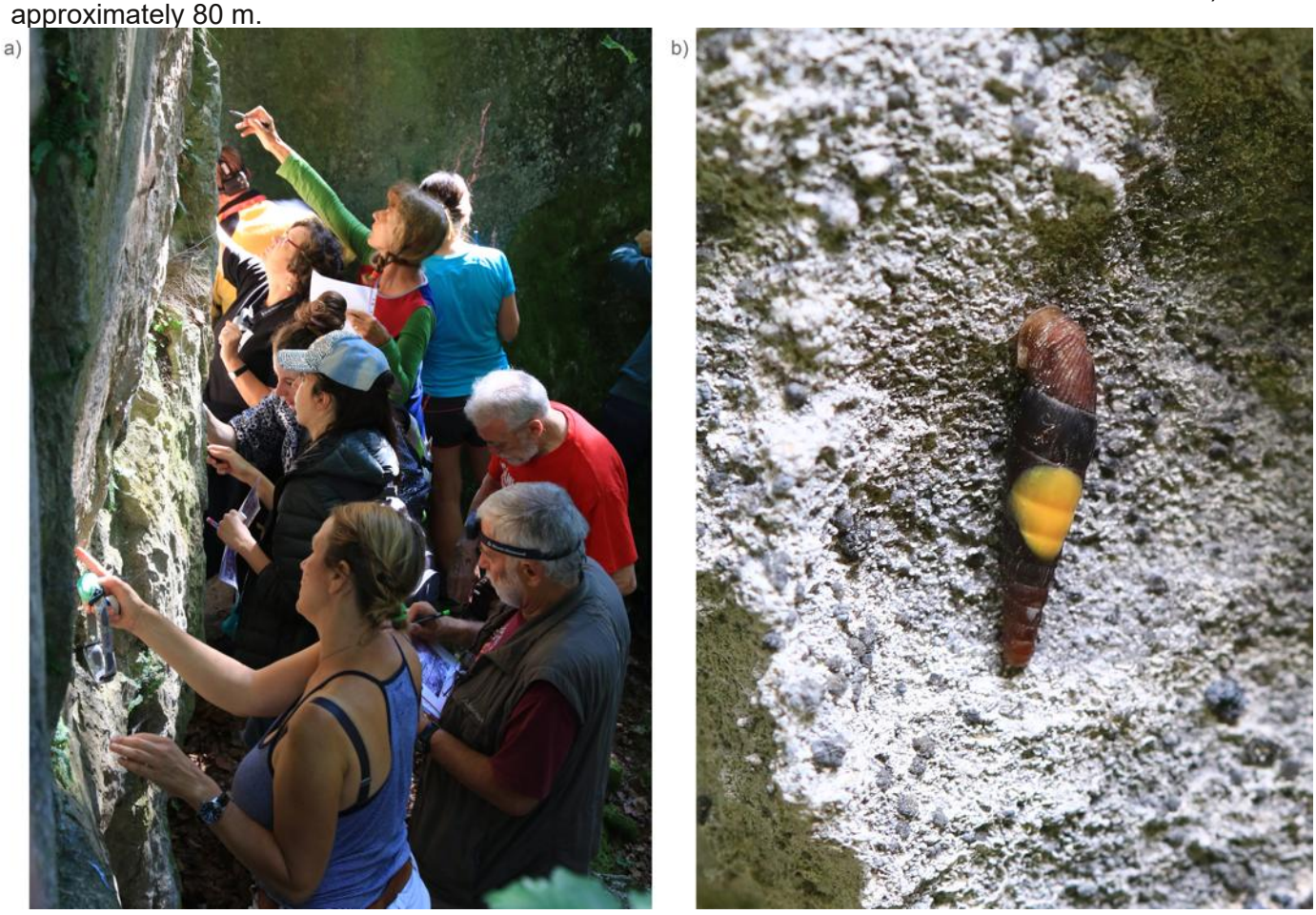

Fig. 2. (a) View of the study site. (b) *Neostyriaca corynodes* marked at section 1

The site studied is approximately 15 m long and is naturally divided into three rock faces with varying exposition (Fig. 1). The entire study area was further subdivided into 10 sections each 1.5 m wide and 3 m high. These sections were marked with chalk on the rock face. On printed photographs of the sections each was subdivided by a grid of 50x50 cm cell size to facilitate recording of the positions of snails (see description of sampling). To allow comparisons between the sampling areas, the same raster was used for all of them. Since it turned out that some peripheral squares could not be screened as they were either partly covered with vegetation (near the ground) or not well reachable, such parts of the sections were identified and excluded from the calculations. Areas with their grids are illustrated in figure 1.

During the period of investigation the weather was fine without rain, average humidity 75-80% and temperatures between 5 – 21 °C, recorded at the weather station Oberkainz nearby (koelblwirt.at/de/webcams-wetterstation-messdaten.html). The microclimate was humid due to pretty much shadowing of the site by trees, the proximidy of a waterfall and small runlets ouzing out at some spots. This became also visible from some of the vegetation (e.g. mosses).

Sampling & marking

On two days (21.8.2017, 23.8.2017, in the following "day 1" and "day 2") between 10:00 – 11:30 a.m. each section was investigated by a team of three people (Fig. 2). Each of the ten teams used different colors for marking. For marking, dots of nail enamel were placed with a fine brush to the shells. Only the few individuals of the large shelled species *Chilostoma achates* were marked with numbers. On day 1 the examiners recorded the positions of the snails with single small letters on their graduated section map. On day 2 the same procedure started, but marked (recaptured) animals were recorded on new copies of the maps with small letters, while new records were marked on the maps with capital letters. To support the observer teams, three additional people formed the consulting team for determination support (e.g. for subadult animals), another two people did a vegetation survey and an "other invertebrate" survey respectively at the study site.

Taxonomic notes

The taxonomy of *Pyramidula* is still under discussion. While Klemm (1974) listed *P. rupestris* for Austria, Gittenberger & Bank (1996) assigned eastern Alpine *Pyramidula* to *pusilla*. According to morphological and genetic results Kirchner et al. (2016) hypothesised that both species might occur in Austria. According to a later study of Razkin et al. (2016) only *P. pusilla* and *P. saxatilis* are assumed to occur in the Eastern Alps. Since morphological assignment is not possible we decided to keep this open and use *Pyramidula pusilla/saxatilis* in this paper. Further molecular studies and more detailed morphological studies are needed to solve this question.

Data analysis

Calculation of species densities were done based on the estimated section sizes (see above).

Vertical distribution of snails on the rock faces (i.e., height of position above ground) were analysed in detail for *Pyramidula pusilla/saxatilis*: A Chi-Square test (degrees of freedom = 3) was performed to test whether *Pyramidula pusilla/saxatilis* was distributed in a non-uniform way over the height zones. For these calculations sections 1.1 to 2.1 as well as 3.1 and 3.2 were used. Sections 2.2 and 2.3 were excluded because of too low nunmbers of individuals found. One section (3.3) had to be excluded from the capture re-capture analysis because of erroneous records on the map of day 2. For sections 1.1 to 2.1 height zones 2 to 5 were included, (parts of the other height zones had been excluded; see above). For sections 3.1 and 3.2, height zones 1 – 4 were included.

Population sizes (N) and their standard deviations were calculated with the Lincoln Index (Mühlenberg 1989): $N = m \times c/r$ (m= number of marked animals at first catch; c= number of animals at second catch; r = number of marked animals recorded at second catch). Standard deviation is the square root of s^2 with $s^2 = (m^2 \times c(c-r))/r^3$.

RESULTS

Species spectrum, frequencies and densities of species

One section (3.3) had to be excluded from the capture re-capture analysis because of erroneous records on the map of day 2. Altogether eight species were recorded at the sampling site. Absolute specimen numbers counted on the first day as well as frequencies of species are given in table 1. The most abundant species was *P. pusilla/saxatilis* followed by *Chondrina avenacea, Neostyriaca corynodes, Orcula gularis*, and *Clausilia dubia*. Three species were found only in very low numbers: *Cochlodina laminata, Chilostoma achates, Petasina unidentata* (table 1). Interestingly, *Arianta arbustorum*, which was recorded at the site in spring 2017, was not encountered at all. *Chilostoma achates* was observed in sections 1.4 and 3.2 (one individual each) on day 1, and in section 3.1 (two unmarked individuals) on the second day. One individual of *Petasina unidentata* was found on day 1 in section 1.2, another one (unmarked) in the same section on day 2, as well as one unmarked individual each

Table 1. Species counts and mark recapture calculations

	Day 1			Day 2			Mark-recapture	
Species	**m**	**%**	**c**	**r**	**r (%)**	**N (calc)**	**s**	**Z (obs)**
Chondrina avenacea	136	28.6	129	109	80.1	161	6.1	156
Cochlodina laminata	3	0.6	3	2	66.7	-	-	4
Neostyriaca corynodes	50	10.5	29	26	52	56	3.5	53
Clausilia dubia	38	8	24	17	44.7	54	7	45
Pyramidula pusilla/saxatilis	196	41.2	252	155	79.1	319	15.9	293
Orcula gularis	49	10.3	30	20	40.8	74	9.5	59
Chilostoma achates	2	0.4	2	0	0	-	-	4
Petasina unidentata	1	0.2	3	0	0	-	-	4
Sum		475	100	472	329			618

Note: m = specimens counted on day 1 at the sampling area (sum of all sections); % = frequencies of species; c= number of animals recorded on day 2; r = number of marked animals recorded on day 2; N(calc) = number of specimens calculated from mark-recapture data (only for species with counts >20; rounded); s = standard deviation; Z(obs) = sum of observed individuals (day 1 plus day 2)

in sections 2.3 and 3.1 on day 2.

Results of day 2 calculated over all sections are also summarized in table 1. The highest recapture rates (80 %) were observed for *Chondrina avenacea* and *Pyramidula pusilla/saxatilis*. Among the frequent species, *Clausilia dubia* and *Orcula gularis* had the lowest recapture rates. In general, numbers of individuals calculated from mark-recapture data are similar to the sum of individuals observed on both days.

Recordings of each section separately are given in table 2. Frequencies of species were not uniform among the sections. Specifically, *Chondrina avenacea* was most frequently observed in sections 1.1 and 1.2., whereas *Pyramidula pusilla/saxatilis* was very abundant in all sections except 2.2 and 2.3.

Dispersal and activity

Based on information of marked individuals there was almost no indication for dispersal of snails from one section to another section during the observation period: On day 2, one individual of *Neostyriaca corynodes* had moved from section 1.1. to 1.2, and one *Pyramidula pusilla/saxatilis* from 3.2 was found in 3.1. Within sections some

Table 2. Species counts and mark recapture calculations for sections

Section/Species	**1.1**	**1.2.**	**1.3**	**1.4**	**2.1**	**2.2**	**2.3**	**3.1**	**3.2**
C. avenacea	28/32/28	40/42/38	14/9/6	9/9/0	13/17/12	13/7/5	2/1/1	5/1/1	12/11/9
	32 (1.7)	44 (3.2)	-	-	-	-	-	-	-
N. corynodes	14/4/3	8/5/4	8/8/8	6/6/6	3/3/2	2/0/0	4/2/2	4/1/1	1/0/0
	-	-	-	-	-	-	-	-	-
C. dubia	4/0/0	3/2/2	2/0/0	3/2/1	3/4/3	8/6/4	9/6/5	2/0/0	4/4/2
	-	-	-	-	-	-	-	-	-
P. pus./sax.	20/31/16	43/46/40	36/38/21	26/34/21	23/40/16	2/3/1	2/2/2	30/34/24	14/24/14
	39 (1.7)	49 (4.5)	65 (4.2)	42 (2.5)	58 (2.9)	-	-	42 (3.7)	-
O. gularis	2/0/0	9/5/5	11/8/7	6/6/4	0/3/0	1/1/1	3/2/0	8/2/0	9/3
	-	-	-	-	-	-	-	-	-

Note: m/c/r: specimens counted at the nine sections on day 1 (m) compared to day 2 (c) as well as marked individuals on day 2 (r); for species with counts >20 the second line shows estimated N calculated from mark-recapture data (rounded; standard deviation in parentheses). *Cochlodina*, *Chilostoma* and *Petasina* were excluded because of too low numbers.

Table 3. Species densities

Section/Species	1.1	1.2.	1.3	1.4	2.1	2.2	2.3	3.1	3.2	d_av	d_calc
Chondrina avenacea	8.62	11.43	3.73	3.35	3.15	4.52	1.14	3.22	4.27	5.04	5.96
Neostyriaca corynodes	4.31	2.29	2.13	2.23	0.73	0.7	2.29	1.78	0.36	1.85	2.07
Clausilia dubia	1.23	0.86	0.53	1.12	0.73	2.78	5.14	0.89	1.42	1.41	2
Pyramidula pusilla /saxatilis	6.15	12.29	9.6	9.67	5.58	0.7	1.14	13.33	4.98	7.26	11.81
Orcula gularis	0.62	2.57	2.93	2.23	0	0.35	1.71	3.56	3.2	1.81	2.74

Note: Densities of individuals per m^2 (counted for the recording on day 1) recorded in each section; d_av = average over all sections. d_calc = densities (average over all sections) based on calculated population size N. *Cochlodina, Chilostoma* and *Petasina* were excluded because of too low numbers.

movements were recorded as positions with snails marked on day 1 were empty on day 2, while on day 2 newly recorded as well as marked snails were found at positions which were empty on day 1. Since snails were not marked individually (e.g. with numbers), dispersal distances could not be measured. However, snails marked on day 1 were frequently found in the same position on day 2, although there is no proof that these were indeed the same individuals.

Capture-recapture

The calculations were based on nine sections (3.3 excluded, see above). Comparing snail counts on day 1 and day 2 resulted, with a few exceptions, in quite similar numbers for all species (table 2). Yet, considering marked and unmarked individuals reveals that sometimes a considerable proportion of snails from day 1 were not recorded on day 2, while new snails appeared. One of the main questions of this study was to assess to which extent numbers of counted snails in a certain area reflect the actual number of individuals. For this task we performed the capture-recapture calculations for each section separately as well as for the whole site. Results for the whole site (3 areas, 9 sections) for all species recorded in numbers >20 are included in table 1, while the results for each section are shown in table 2. In general, calculated numbers are similar to the actually counted individuals. However, for *Pyramidula pusilla/saxatilis* the calculated values were considerably higher in some sections.

Vertical distribution of *Pyramidula pusilla/ saxatilis* on the rock face

Besides the fact that *Pyramidula pusilla/saxatilis* and *Chondrina avenacea* apparently were non-uniformly distributed among the sections (see table 2) and even were almost absent in some sections, there seemed to be an uneven distribution regarding the height where they were positioned. Height distribution was calculated for the most abundant species *Pyramidula pusilla/saxatilis* which was mostly absent in the first zone (50 cm above ground) and most abundant in zones 3 and 4 (100 – 150 cm above ground). To test whether there was a significant preference, we performed a Chi-Square test for the sections 1.2 - 2.1. A significant deviation from uniform distribution was found in sections 1.2, 2.1 and 3.1 ($p<0.001$), in section 3.2 ($p<0.01$) as well as in section 1.1 in ($p<0.05$). Over all five sections there was a highly significant result indicating non-uniform distribution ($p<0.001$). Although in sections 3.1 and 3.2 the pattern seemed similar, they could not be included in the calculation since the species was present only in three height zones.

Remarks on sampling site – characterization of vegetation cover and arthropod fauna

The dominant tree species in the immediate vicinity of the studied location were *Fagus sylvatica* and *Picea abies*. Additionally saplings of other woody species could be found, e.g. *Fraxinus*

excelsior, Acer platanoides, Sorbus aria, Ulmus glabra and *Sambucus nigra*. Herbaceous plant species in the understorey were represented by *Aruncus dioicus, Lactuca muralis, Lilium martagon, Helleborus niger, Sanicula europaea, Adenostyles alliariae, Geranium robertianum, Oxalis acetosella, Mercurialis perennis* etc. and ferns like *Polypodium vulgare* and *Dryopteris filix-mas*. Limestone blocks were densely overgrown by bryophyte species like *Hypnum cupressiforme*.

Rock face 1: This part of the rock site was almost vertical with a few narrow crevices. The vegetation cover amounted to approximately 1% only, restricted to the crevices. The most frequent species was *Asplenium trichomanes*, a very common rock dwelling fern. Further observed plant species were: *Asplenium ruta-muraria, Lactuca muralis, Primula auricula, Kernera saxatilis, Hieracium murorum, Carex* spp.

Rock face 2: This rock face was inclined to approximately 75 degrees and exhibited a dense moss cover to about 60 % of the area. Due to the less extreme situation humus accumulation allowed other plant species to occur, some of them taller growing species. We observed spruce, maple and elder seedlings, *Geranium robertianum* and *Aruncus dioicus* which are not characteristic for steep rock habitats. As representatives of rock inhabiting species e.g. *Asplenium trichomanes* and *Kernera saxatilis* were present.

Rock face 3: The almost vertical third rock face was covered by vegetation to approximately 5%. Crevices were slightly more prominent compared to rock face 1. The following species were observed: *Asplenium trichomanes, Asplenium ruta-muraria, Potentilla clusiana, Kernera saxatilis, Erica carnea, Hieracium murorum, Carex* spp. and some grass species.

Arthropods of the following groups were observed: spiders, harvestmen, woodlice, pill millipeds (*Glomeris pustulata* and *Glomeris hexasticha*) and jumping bristletails (*Machilis* sp.). Web building spiders were observed in nearly every bigger rock fissure except those located at wet parts of the rock (section 3.1). Woodlice were spotted frequently on the rock face and also in high numbers in the dry leave litter at the foot of the rock. Pill millipedes were found at the sunny parts of rock face 3. Both woodlice and pill millipedes are known for their preference of environments rich in lichens and limestone.

DISCUSSION

Species spectrum, frequencies and densities of species

The spectrum of taxa observed comprised species common in the area and this particular environment. Some of the species were more generalists. Half of the species are mainly rock dwelling or rock-associated species: *Pyramidula pusilla/saxatilis*, *Chilostoma achates* and *Orcula gularis*, and *Chondrina avenacea*. The fact that numbers of individuals calculated from mark-recapture data were similar to the sum of individuals observed on both days suggests that the snails were quite active and visible because of good seasonal and climatic conditions.

Whether species densities were influenced significantly by co-ocurrence of other snail species would be interesting to be analysed for such a relatively high number of species (comp. Baur & Baur 1990). But apparently, as our study shows, population densities are highly dependent on the microhabitat (e.g. almost no individuals on the moss-covered areas).

Mobility and horizontal dispersal

Although for some species observed numbers were quite small, it was apparent that with the exception of *Chilostoma achates* and *Petasina unidentata* the other species were rather immobile in the observed time slot and environment. Nevertheless, it was not possible to calculate distances of movements because the snails were not marked individually. From the distribution pattern of snail frequencies at the two study days and from the very few records of individuals crossing from one to a neighboring section, we deduce that mobility and dispersal tendency for the frequent and small species is very low. From our observations we estimate that activity did not exceed more than few centimeters (within 2 days).

The low dispersal activities of the investigated clausiliids are apparently as low as or even lower than those recorded in a former study for *Cochlodina laminate* by Junker (2015). The same can be said for *Chondrina avenacea*, which has similar low activities with maximum 0.5 m per day, which were also reported for *Chondrina clienta* by Baur & Baur 1995). But we assume that activity might vary with altering climatic and environmental conditions or including seasonal migration as indicated by Junker (2015) for *Cochlodina laminata*. Furthermore, snails may drop down from steep structures or be dispersed passively by other vehicles. At the study site it is planned to test individual marking methods (Henry & Jarne 2007) and to use this to acquire more reliable data for particular species.

Non-uniform distribution

Apparently, distribution of species and individuals was not uniform, with respect to the three rock faces as well as concerning vertical distribution and positions within sections. These differences can be explained by different vegetation cover, particularly the dense of the moss layer. In section 2.1 species occurrence as well as specimen counts were in the same range as in other parts of the whole site, while in sections 2.2 and 2.3 much lower numbers of most species were found. These two sections are characterized by extensive covering by moss as well as larger plants like trees and shrubs. Only one species, *Clausilia dubia*, was found in higher numbers in sections 2.2 and 2.3 compared to the other sections. However, it was found mainly on the lower parts of a tree trunk which grew amidst the rock. In general, only a few snails were found on the moss at all, while most individuals were encountered on the rocky surface between moss patches.

Overall, observers recognized that snails were distributed preferentially near crevices or otherwise structured parts of the areas. While this seems quite reasonable from an ecological point of view and considering the low mobility, it is not possible to quantify such site preferences with the present study design.

Concerning differences in the observed height distribution of *Pyramidula pusilla/saxatilis,* one might argue that it could be due to a sampling artefact, since the height with the densest occurrence corresponds with the most convenient position for collecting for adult humans. However, we do not regard this as a likely explanation because the observers were instructed to specifically take care to avoid such a bias. Presently it is not possible to put forward a reasonable hypothesis for the observed bias in the distribution of *P. pusilla/saxatilis*. Several factors could influence the distribution, e.g., microclimate, microhabitat factors (vegetation, food availability, e.g., lichens) or predator interactions.

Similar distribution patterns (i.e., height zones; structured/unstructured areas) might hold true also for the other species, but the specimen counts were too low to address this issue by statistical tests in the present analysis.

Mark-recapture analyses

In general, the recapture rate was high, but the results have to be differentiated. For three species (*Cochlodina laminata, Chilostoma achates* and *Petasina unidendata*) counted numbers were too low to draw any conclusions. For *Chondrina avenacea, Neostyriaca corynodes, Clausilia dubia,* and *Orcula gularis* there was a high recapture rate and together with the observation that snails almost never crossed borders of sections one can assume that they are quite immobile.

For the smallest species, *P. pusilla/saxatilis*, the calculated values were considerably higher than the counts on day 1. This can be explained by higher activity / mobility but might also be due to low visibility and finding probability. Nevertheless, also for *P. pusilla/saxatilis*, only one individual was recorded to cross a section border. Thus, it appears likely that they may frequently hide in crevices.

Critical comments on methods

For further studies it should be tested if the nail polish (solvent or pigments) might harm the snails or negatively influence their mobility. Similarly, any potential influence of the chalk marking on the rocks on snail movements should be tested under standardized conditions.

As a matter of fact, with this study design we surveyed a comparatively small area only and it was not possible to evaluate the distribution patterns of the various species in the upper regions of the rock face. We do not know whether in higher elevations above the investigated area the distribution is similar and according to the results from our study it might vary considerably. Therefore, it is not possible to extrapolate numbers for the “whole population”. Furthermore, seasonal aspects were not covered. However, we could at least get first insights into population densities as well as relative frequencies of several co-occurring rock-dwelling snail species.

The monitoring was possible only with a large group of investigators. But, such a survey would not have been possible with completely unexperienced people. All of the persons involved had some experiences in monitoring and observing snails. Nevertheless, the differentiation of species, especially of juveniles, might sometimes be problematic. We did not exclude juveniles as this might have resulted in too low counts. Moreover, for assessing whether a specimen should be regarded as adult the need of manipulating individuals would have been counterproductive, since we were striving to intervene as little as possible. It has to be mentioned that during the survey snails only rarely fell down when being marked. In general, we tried to prevent possible problems of species assignment by including taxonomic experts as supervisors.

For similar studies as presented here it is essential to employ a high number of people and in principle such surveys appear attractive for “citizen science” projects. Yet, we recommend to involve experts and trained people as well as to provide adequate training for all participants.

Conclusion

The present pilot study provided insights into occurrences of snail species and their relative frequencies on a rock face in the eastern Alps. Species densities and populations sizes estimated from the data varied among sections along the rock face. The most relevant factor seemed to be moss coverage. Areas with moss proved to be almost completely devoid of snails. Mobility and dispersal tendency for the frequent and small rock-dwelling species is very low and the re-capture rate was in general high. *Chilostoma achates* and Petasina unidentata occurred only in low numbers and were quite mobile. Mobility even of small snail species could be further explored by individual marking using various colors. Moreover, the uneven distribution concerning height above ground as well as with respect to structuring should be investigated in detail including a higher number of sites.

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