First data on population estimates and dispersal of *Montenegrina subcristata* – a field study at Virpazar, Montenegro

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Received 14 November 2019 | Accepted by V. Pešić: 27 December 2019 | Published online 31 December 2019.

Abstract

*Background.* In this study a population of the rock dwelling terrestrial gastropod *Montenegrina subcristata* was monitored over one season and data about life cycle, population density and dispersal were gathered. Three study sites (A, B, C) near Virpazar, Montenegro were selected. Snails were categorized into three size classes. (1) The smallest juveniles were counted but not marked because of their tiny and dainty shell, middle sized snails (2) were marked with a dot and (3) larger subadults and adults were marked with an individual number. The sites were observed 25 times from April to October 2017. The study sites were equipped with data loggers to register microclimate data like temperature and humidity. Based on counts and recapture counts population estimates were calculated. Positions of the snails were recorded throughout the season and minimum distances between each two observations were calculated.

*Results.* Small juveniles (not marked) were observed in high numbers at the beginning of the season and disappeared during summer. Site C had to be excluded from the calculations because snails nearly disappeared as early as the second visit. Population size estimations of sites A and B provided similar results for the beginning of the season, whereas for June the high estimates stood in high contrast to the number of observed snails in that period. Concerning “minimum distances” (MD; distance between two subsequent observations), the majority of MDs with a 1-week interval resulted in 0–0.1m. Yet, some individuals were more mobile, with sums of MDs over the season of up to 8.0m. The sum of MDs over the season was on average 1.6 m (sites A+B).

The temperature and humidity curves of the data loggers showed a seasonal pattern. The average temperatures of all three sites were rather similar. However, daily oscillations in temperature and humidity were high in some periods and differed between sites. In site C temperature and humidity extremes and fluctuations were pronouncedly higher, with the highest temperatures reaching more than 60 °C and relative humidity dropping each day below 3.7% in June.

*Conclusions.* Dispersal ability is in general low but single individuals might cover distances of at least several meters over the season. Together with further observations we conclude that fluctuations of population size can be considerable and might be strongly influenced by climatic conditions. On the other hand, also population estimates may be influenced by climatic conditions. This study provided first hints to assess the potential of migration, local extinction and recolonization in *Montenegrina* and other rock dwelling snails.

*Ecologica Montenegrina*, 26, 2019, 147-165
**Key words:** rock-dwelling snails, mobility, population size, microclimate, ecology.

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**Introduction**

Population size and dispersal of individuals are basic information in population ecology, population dynamics and evolutionary biology. Density as well as dispersal ability and behaviour affect the genetic structure of a population and the potential to colonize new habitats. Limited dispersal favours, for example, local adaption, can lead to restricted gene flow between populations, and in turn may enhance reproductive isolation. Speciation processes could be the consequence (e.g. Mayr, 1963; Futuyma, 1990). In some land snail populations (of the genera *Arianta* and *Cepaea*) dispersal and migration of the individuals were found to be density-dependent (Greenwood, 1974; Oosterhoff, 1977). However, only few rock dwelling European land snail species have been covered in this respect. *Balea perversa* and *Chondrina clienta* have been studied in Sweden (Baur & Baur, 1990, 1995; Schmera et al., 2015) and *Albinaria* in Greece (Giokas & Mylonas, 2002, 2004; Giokas et al. 2005). These studies showed dense populations with low dispersal abilities, if compared with other e.g. helicid land snails (Kleewein, 1999). Yet, the ground and rock gravel dwelling helicid *Cylindrus obtusus* showed even lower activity (Bisenberger et al., 1999).

The study organism of the present investigation, *Montenegrina subcristata* (Pfeiffer, 1848) is a rock dwelling clausiliid land snail with a distribution in the western Balkans. Taxonomic and phylogenetic studies revealed that it is the most widely distributed species of the genus *Montenegrina*, which is scattered in many – presumably isolated – populations from Montenegro to northern Greece (Fehér & Szekeres, 2016). Since taxonomic, phylogenetic and phylogeographic studies suggest a remarkable radiation of the genus in a rather restricted area and speciation processes within syntopic or at least neighbouring populations (Fehér & Szekeres, 2016; Fehér et al., 2018; Mason et al., submitted; De Mattia et al., submitted), the question of population dynamics and dispersal abilities is of particular interest. The dependence on limestone rocks and the presumably island like distribution has been put forward as an explanation for the high morphological and genetic variation of *Montenegrina*. Yet, while isolated habitats offer a plausible cause for the taxon richness of the genus, neither population densities nor dispersal ability have been estimated in *Montenegrina*.

Population densities may influence reproduction rates, niche competition, genetic structure and dispersal. Up to now no data exists about any of those parameters in the genus *Montenegrina*.

The aim of the study was to obtain first insights into biology, ecology and dispersal ability of *M. subcristata*. By monitoring the species over a season at three sites we wanted to get data on species abundances, movements, growth rate and life cycle. We also gathered temperature and humidity data at the three sites and tried to connect them with respect to the abundances of snails at the three sites. One of the main tasks of the study was to obtain estimates of population size by mark-recapture methods.

**Material and Methods**

**Sampling site, monitoring regime**

Three study sites were selected in an area at Virpazar (N 42°15´05´´; E 19°05´17´´), Montenegro (sites A, B and C) with 16 m² (each, site A and site B), and 10 m² (site C) in size. Sites A and B were located side by side with 1 m distance, while site C was located 11 m above (Figure 1). Sites were selected according to the following criteria: suitable rock environment, easy to access, feasibility (possible to survey within 1 hour), few human interference expected, many snails present at first visit. The three sites were visited once a week on average between April 3rd and October 15th 2017 and screened for snails. In addition to the defined rock sites, which were surveyed in detail including crevices as far as accessible, also the surrounding area was screened to see whether there were numbered adults/subadults (including dead ones) present. Further single observations are summarized under additional observations. General data (date, persons involved, and weather conditions) were protocolled. Tiny juveniles were only counted, while larger ones were marked only with a dot, and subadults and adults were marked individually with numbers. At each visit snails were counted and the positions of numbered individuals were documented on photographic maps. The areas adjacent to the threes sites (~0.5 m distance from the borders) were also surveyed concerning occurrence of numbered snails. Dead individuals beyond the three sites were collected and counted. To get an overview of
the size ranges of adult snails, 83 snails collected dead in the surrounding of the study area were measured and numbers of whorls were counted (inventory number of those snails in the mollusc collection of the Natural History Museum Vienna: NHMW-MO 112355). After 15th October, the site was visited 14 times: December 2017, January to October 2018 (see additional observations).

At each site three data loggers (iButton, Maxim Integrated Products), two recording temperature, and one for humidity and temperature, were placed in sheltered positions (in crevices), one near the ground and two at more elevated positions.

Data were read out once a month. General problems arose with the data loggers, which had to be replaced several times because of failure. This resulted in gaps of the recordings (see results).

Figure 1. Study area with three study sites (A, B, C). Note that due to the perspective view site B and C appear much smaller.

Population estimates and densities
For estimates of population size, calculations of marked snails were performed with different formulas of mark-recapture protocols. Mark-recapture methods require that individuals encountered at the first visit are counted and marked and then released back into the environment. At the next visit, unmarked and marked individuals are counted. Assuming that the proportion of marked individuals equals the proportion of caught individuals, one may calculate an estimate of the population size. Most mark-recapture methods assume that the system is closed; which means no individuals leave or enter and they do not reproduce (see below). In our study system we could not expect a closed population as snails may move in or out the study site. Yet, it was assumed that the number of incoming or outgoing individuals was low (which was confirmed by the low number of snails found in the neighbouring site).

In our study system, we dealt with different cohorts: (1) "small juveniles": juveniles too small and dainty to mark (up to 8 mm), (2) "dotted juveniles": juveniles marked with a dot (8 ≤ 14 mm), (3) "numbered subadults/adults": subadults and adults individually marked with numbers (14 ≤ 25 mm) (see Figure 2). It is clear that the abundances calculated for these groups reflect different proportions of the population, which vary over the season. Thus, it must be considered that calculations of abundances based on any of these cohorts cannot reflect total population size. Nevertheless, the calculated numbers may be compared with mere counts and calculated numbers can be compared between sites.
Population estimates were done with the spreadsheets of Panks and Jungck (2007). Population estimates based on the formulas of Lincoln-Petersen (LP) and Bailey’s modification of Lincoln-Petersen are only applicable for closed populations (Bailey, 1951; Roff, 1973; Krebs, 1989). These population estimates were calculated only for the data of the first recapture campaign. Since there was an interval of only five days between capture and first recapture we assumed that changes induced by birth, death, growing and migration were negligible.

For the subsequent visits, the Jolly-Seber (JS) model (Jolly, 1965; Seber, 1965) was used to estimate abundance of subadults/adults over the year. JS is also applicable for open populations (including birth, death, immigration, and emigration) (Krebs, 1989). For JS calculations, it is assumed that unmarked animals have the same survival probability and probability of capture as marked animals, i.e., that newly captured unmarked animals are a random sample of all animals in the population. Furthermore, we can assume that animals retain their tags throughout the season. Very rarely, we encountered snails needing refreshment of their marks; even after one year numbers on individuals found were readable. For the JS calculations, dotted individuals could not be used since, after the second visit, it is not clear any more at which time recaptured individuals had been marked.

Numbers of individuals divided by the size of sites (individuals/m²), hereafter called "densities", were calculated for raw snail counts as well as for the various population estimates obtained by the LP and Bailey’s modification of LP methods.

**Dispersal**
For snails observed at least two times, minimum distances (MD) were calculated between each two subsequent observations. This minimum distance is only a very rough estimator for movement of the snails. Clearly, even within one week, individuals may move a lot and the positions of two observations may be much closer than the distance the snail actually covered. Sometimes several weeks passed until an individual was observed the next time, and therefore, we considered the MD as the only reasonable value representing a

Figure 2. *M. subcristata* shell-size classes: (A) small juveniles (too small to mark), appr. 8 mm shell height), (B) dotted juvenile, appr. 12 mm; (C) numbered adult, appr. 20 mm.
distance that the individual evidently must have covered. It thus provides a proxy about the dispersal potential.

For each numbered snail (subadult/adult) observed, the position on the grid was translated into a position within a coordinate system (x/y). Exact positions of snails within each grid square were not taken into account, instead integer coordinates were used. This allowed a simple calculation of distances between two observation points. For calculation of distances the online tool polygon calculator (https://rechneronline.de/pi/einfaches-polygon.php) was used. The error of max 35 cm due to this standardised position in the grid was considered as insignificant compared to the error due to missing observations between two observation dates.

A temporal aspect in the sense of a "dispersal rate" was not considered in our calculations due to the above mentioned uncertainties. Yet, we calculated MDs separately for the smallest time interval, i.e., for all observations with an interval of approx. 1 week. Moreover, MDs of all subsequent observations (irrespective of the time interval) were calculated. Finally, for each individual the sum of MDs over the season was calculated.

Results

General results and numbers of individuals

The procedure of the monitoring worked in general well, except problems with the temperature loggers (see below). The labels on the snails proved to be quite stable and only rarely they had to be refreshed. Even one year after the monitoring period 2017 individuals with readable numbers were found.

Table 1 shows an overview of individuals counted at the three sites over the whole season. The three sites differed considerably, as exemplified with the mere counts of subadult/adult individuals (i.e., snails marked with numbers): At site B the number of individuals (127 numbered subadults/adults) was only 53% of site A (241), and at site C the number was extremely low with only 10 individuals. Due to this low number, site C was excluded from all subsequent analyses.

At both sites the majority of numbered subadults/adults were observed one or two times only. Four snails at site A were encountered 6 times and at site B one single snail was found even 11 times. One has to keep in mind that, as a matter of fact, in Table 1, due to the re-captures of marked snails and due to the growth of snails over the season (small juveniles, dotted juveniles, numbered subadults/adults), many individuals were recorded more than one time, e.g., as small juveniles (too small to mark) and later as juveniles that were marked with dots or, some of them, even later with numbers. Thus, although it appears not meaningful to sum up these numbers over the season, they are shown (marked with an asterisk) as they reflect general differences in abundances of the various age classes between the three sites.

Table 1. Summary of individuals counted at the three sites.

|                  | A     | B     | C     |
|------------------|-------|-------|-------|
| Small juveniles  | 337   | 132   | 55    |
| Dotted juveniles | 402   | 175   | 2     |
| Juv. dotted recapture | 82   | 54    | 0     |
| Numbered subadults/adults | 241 | 127   | 10    |

Times observed

(numbered individuals):

|        | A | B | C |
|--------|---|---|---|
| 1 time | 159| 70| 7 |
| 2 times| 48 |30 | - |
| 3 times| 13 |12 | - |
| ≥ 4 times | 8 | 11 | 3 |
| Max. times observed (n) | 6 (4) | 11 (1) | 8 (1) |
| Numbered dead observed   | 25 | 23 | - |
**Note:** At each visit small juvenile individuals < 8 mm in shell height (too small to mark) were counted ("small juveniles"). Juveniles of 8–14 mm were marked with dots ("dotted juveniles new") and already dotted juveniles ("dotted juveniles recapture") as well as subadults and adults (> 14 mm) marked with numbers ("numbered subadults/adults") were also counted. The numbers summarise the counts over the whole season to allow comparison between the three sites (for * see text). For numbered individuals that were repeatedly observed the times of observations are given (n = number of snails).

The individuals counted over the season are shown in Fig. 3 differentiating the various age categories. At site A after an initial increase of small juveniles, they dropped in numbers, while the counts of dotted juveniles as well as of numbered subadults/adults increased. In each category the counts decreased considerably after the beginning of June. After a second increase on June 18th, all counts remained very low (< 10) on each observation day. At site B, the pattern is not so pronounced, but is similar, except for the fact that much more juveniles were dotted at the first visit compared to site A. Fig. S1 shows diagrams where, for each observation day, the numbers of newly marked and already marked (recaptured) individuals are shown separately (see Supporting Information).

**Figure 3.** Snail counts at site A (above) and site B (below); juv. small = small juveniles (too small to mark); juv. dotted = dotted individuals; subadults and adults = numbered subadults/adults.

When summing up the numbers of individuals (of all categories) counted at each observation date, it becomes apparent that the numbers decreased abruptly after May 16th in site A, while in site B the decrease in total counts was observed already starting in April (Fig. 4).
Dead individuals
At site A, altogether 25 (10%) of the numbered snails were later found dead, the first recorded on June 5th and the last eight recorded on October 15th. At site B, altogether 23 (18%) numbered dead individuals were
found, 11 of them in June (the first dead one recorded on June 5th) and the last on October 15th. At site C only four dead individuals marked with numbers were found: two on October 1st and two on October 15th.

**Growth rate**

Nine snails that had been marked with a dot were later found again and numbered. Although the exact dates when those snails had been dotted were unknown, we could deduce the range for a minimal growth rate. For the dotted snail recaptured on May 10th (and then numbered at that day) the growth rate was at least 1 whorl per 5 weeks assuming that it received its dot at the first day April 4th (if the first capture of this snail was at a later date, the growth rate would be even higher). For two other snails the growth rate would be at least 2 whorls in 6 weeks (again with the same assumptions). The remaining six snails were found 7–17 weeks after April 4th which would blur the estimate, because of the long period between first sampling day and recapture. As this did not allow meaningful conclusions, they were not considered.

Snails were considered as adults when the lip was developed. The size of adult individuals ranged broadly from 19.1–24.7 mm and also the number of whorls varied (9–11).

**Population estimates**

For the dotted juveniles, population estimates according to the LP and Bailey’s modification of LP methods could be done for the first two visits for sites A and B. For subsequent visits dotted juveniles could not be used for the calculations any more since for recaptured individuals, after the second visit, it was not clear any more at which time point they had been marked. For the numbered subadults/adults these indices were also calculated. Table 2 shows that the estimates at site A were higher than those for site B (conforming to the real counts), and that the estimated numbers of individuals marked with numbers were approximately 1/10 of the dotted ones.

| Site     | Dotted juveniles | Lincoln-Petersen | Bailey’s       |
|----------|------------------|------------------|----------------|
|          | N                 | 269 (17)         | 242 (15)       |
|          | Standard error    | 81               | 72             |
|          | Confidence interval (95%) | 111-428 | 100-383 |
| A        | N                 | 216 (14)         | 200 (13)       |
|          | Standard error    | 55               | 51             |
|          | Confidence interval (95%) | 109-322 | 101-299 |
| B        |                  |                  |                |

Table 2. Population estimates of sites A and B for dotted and numbered individuals (April 2017). Number of individuals per m² are given in parentheses.
Applying the Jolly-Seber (JS) model (Jolly, 1965; Seber, 1965) to the data of numbered subadults/adults resulted in much higher estimates (max. 447 individuals at site A; 545 site B) than any other counts or calculations (Fig. 5).

**Figure 5.** Population estimated according to Jolly-Seber for site A (above), site B (below). Y axis: estimated number of individuals.

**Population densities**
Numbers of individuals divided by the size of areas (individuals/m²), hereafter called "densities", were calculated for raw snail counts as well as for the various population estimates obtained by the LP and Bailey’s modification of LP methods (Table 2). These values are much higher than those calculated from the total counts (small juveniles, dotted juveniles, numbered subadults/adults; see total counts Fig. 4): At site A densities ranged from 6–9 individuals per m² between April 4th and May 16th and then dropped to one to 2–3 individuals per m² until end of June. After July 2nd densities were < 1 individuals per m² with one exception (1.3 individuals per m² on September 10th). At site B high densities were observed in April only: 5–7 individuals per m² at the first two visits. After that densities ranged from 1–3 and after July 9th they remained < 1 individual per m².

The densities calculated from the JS estimates were at the beginning (in April) similar to those obtained from the other estimates ≤ 2 individuals per m² (site A) and < 5 individuals per m² (site B). In summer, when JS resulted in maximum estimates, the corresponding densities were rather high: 30 (site A) and 34 (site B) individuals per m². These values seem unrealistic (see discussion).
Dispersal - positions and movements
Minimum distances (MD) were calculated for snails observed at least two times, i.e., the distance between two subsequent observations. As sometimes snails were found at the same point at subsequent observations, the MDs reported below (Fig. 6) comprise also zero distances.

At site A, the 52 minimum distances (MDs) of all observations with a ca. 1-week interval ranged from 0–2.85 m with 23 MDs ranging between 0–0.5 meters (m). These MDs were categorized and the frequencies counted (Fig. 6). The majority of individuals (34) at site A had MDs in a 1-week interval ranging between 0–1.0 m. For site B there were 63 MDs calculated from a 1-week interval observations ranging from 0–2.93 m. The majority of individuals (40) had MDs ranging between 0–0.5 m.

Figure 6. Minimum distances (in meters, x axis) of numbered individuals (y axis: absolute numbers of individuals) from site A and B of all observations with a ~1-week interval.

MDs calculated over all subsequent observations at site A (irrespective of interval) ranged from 0–3.25 m. Again, the majority of MDs was small: 42 of 104 MDs were ranging between 0–0.5 m (Fig. 7). For site B, MDs calculated over 105 subsequent observations ranged from 0–4.37 m, with the majority (56) of MDs ranging between 0–0.5 m.

Figure 7. Minimum distances (in meters, x axis) of numbered individuals (y axis: absolute numbers of individuals) from sites A and B, over all subsequent observations.
Finally, for each individual, the sum of MDs over all subsequent observations (over the season) was calculated (Fig. 8). At site A, 63 sums of MDs ranged between 1–4.6 m and 36 ranged between 1–1.5 m. At site B, 54 sums of MDs ranged between 0–5.1 m and again the majority of sums of MDs ranged between 0–1.5 m.

![Figure 8. Sum of MDs (in meters, x axis) over all subsequent observations (over the season) of numbered individuals (y axis: absolute numbers of individuals) from site A and B.](image)

To summarize, the majority of individuals moved around within a small area over the season (sum of MDs over the season ≤ 1.5 m). Yet, there were some more mobile individuals for which longer distances (MD over season) were observed. Furthermore, there were six individuals that moved from site A to B (or even back). For these snails, MDs were calculated separately: sums of MD (over season) for these individuals were high: 5.0, 3.5, 4.6, 5.8, 4.4, and 5.1 m. Two individuals that moved from site B to A had sums of MD of 8.0 and 4.5 m.

In general, individuals were moving most during the rainy periods in April and May. In summer their mobility was low and they were mostly estivating, even during short rainy periods.

**Temperature and humidity**

Temperature and humidity loggers were in their positions on the rock faces from April 4th to December 24th 2017 with some short interruptions (e.g., when defect loggers were replaced). Three of the loggers were replaced (one at site A and two at site C). In addition, there were shorter periods with missing data (e.g., at site B no humidity data were recorded in a period of eight days in May) and the humidity sensors stopped to function at all in the middle of October at all three sites. This resulted in some gaps in the recordings, particularly at site C. Figure 9 presents the temperature and humidity profiles of the three sites.

While the mean values for all loggers are very similar (22.2–24 °C) with only one logger at site C having a slightly higher value (25.9 °C), the ranges reveal more meaningful insights. At sites A and B temperatures were rather similar both between loggers at each site as well as between sites (Table 3). In contrast, at site C maximum temperature values were considerably higher for two of the loggers reaching even 50.0 and 60.5 °C. The hottest period was from May 31st to July 15th when almost every day the
temperature maximum at logger 1 was > 50 °C. At site C, the highest temperature of > 50 °C recorded by logger 3 was in October, but this might be considered as an artefact (Figure 9). This logger recorded only lower temperatures even in the hot period (mostly slightly below 40 °C). Logger 3 at site C failed to record in the hottest period.

Figure 9 illustrates that the daily oscillation between minimum and maximum temperature was rather homogenous at all loggers at sites A and B and only rarely exceeded a range of 20 °C. In contrast, at site C logger 1 frequently revealed a daily range of 30 °C, sometimes even 40 °C in the hot period in June and July.

Table 3. Temperatures (minimum, mean and maximum) measured at the three sites (three loggers at each site). NA = missing data.

| Logger | Min.  | Mean  | Max.  | NA   |
|--------|-------|-------|-------|------|
| A1     | 1.08  | 23.37 | 43.55 | 1004 |
| A2     | 5.10  | 23.96 | 43.60 |      |
| A3     | 4.57  | 23.71 | 42.60 |      |
| B1     | 2.10  | 23.36 | 44.03 | 4    |
| B2     | 5.06  | 23.81 | 46.55 | 4    |
| B3     | 4.52  | 23.91 | 44.12 | 33   |
| C1     | 7.08  | 25.90 | 60.52 | 2192 |
| C2     | 2.07  | 23.86 | 44.09 | 102  |
| C3     | 4.57  | 22.12 | 50.04 | 1027 |

Table 4. Relative humidity (%; minimum, mean and maximum) measured at the three sites (one logger at each site).

| Humidity | min | max | mean |
|----------|-----|-----|------|
| Site A   | 14.16 | 100 | 64.06 |
| Site B   | 14.35 | 100 | 46.62 |
| Site C   | 0    | 100 | 54.29 |

Concerning humidity, mean, minimum and maximum values are similar (Table 3) except the minimum value of zero at site C. But again it is more interesting to look into the profiles in detail. In the humidity profiles of the three sites, there are periods with high daily ranges, specifically in June and July. Between beginning of June and middle of July daily humidity ranges were very high. At site A daily ranges were often more than 70 percentage points and in site C the range frequently exceeded 50 percentage points in that period. In site B these oscillations were least pronounced with highest ranges in spring and extreme stable humidity starting with the second week of August. Finally, all three humidity loggers recorded periods where 100 % humidity was continuing over several days.

Additional observations

Snail Counts 2018/2019

Repeated visits of the study site during the subsequent seasons (end of 2017, 2018, and 2019) revealed a considerable decrease in numbers of living snails. While in the winter season (December 2017, January and March 2018) no living snails were observed, many larger juveniles, subadults and adults were recorded in early April 2018 (Site A: 87; site B: 12, site C: 6). Subsequently, during the next visits, the numbers decreased rapidly and were consistently zero from July on. Also during a few visits in 2019 no living individuals of Montenegrina were observed at the site, but at October 5th few apparently fresh dead shells were recorded. Most striking was the total absence of small juveniles during the visits in 2018 and 2019.
Figure 9. Temperature and humidity profiles at sites A, B, and C between April and December 2017. TA = temperature at site A (three loggers), TB = temperature at site B (three loggers), TC = temperature at site C (three loggers). HA, HB, HC = humidity profile at sites A, B, and C, respectively. Some missing data are due to temporal failure of some loggers. Humidity loggers stopped to function completely in the middle of October at all three sites.
Recaptures
In 2018 two snails marked with individual numbers were recaptured alive: A18 and A80. The time span between marking and recapturing was between 11 and 12 months. One of the individuals (A80) was recorded 3.5 m outside the study site, where it was first recorded.

Discussion
We provided here first data on the population size and dispersal of a Montenegrina species and thus add information to the otherwise scarce knowledge regarding these aspects in clausiliids. Our study exemplifies that observations in a natural environment are severely limited by local factors and thus one should be cautious to draw general conclusions. For example, the three sites selected for the study appeared similarly appropriate. Yet, it turned out that at site C the number of individuals dropped after the first visit and almost no individuals were observed over the season. Another difficulty arose from the fact that the selection of study sites was somehow arbitrary because of lacking knowledge concerning the migratory range. Finally, the study sites were defined also from a practical point of view. The areas were rocks with little vegetation that allowed easy surveys. The upper boundaries of the study sites were easily accessible and it was feasible to screen the three sites within one visit. Several difficulties will be addressed in the discussion below, and the experiences gathered in the present study would allow to set up a subsequent study in a more sophisticated way.

Population size – counts and estimates
Two approaches were used to obtain data on population size: (1) simple counts of individuals and (2) estimates based on mark-recapture methods. Since we wanted to trace movements of single individuals it was necessary to mark them individually. Yet, this was possible only for subadults/adults, but not for juveniles. We had three cohorts: small juveniles (too small to mark), dotted juveniles, and numbered subadults/adults (individually marked with numbers). While it was possible for each visit to sum up the counts of the three cohorts, the mark-recapture analyses allowed estimates either for two subsequent visits only (for dotted and numbered individuals) or, with the JS method over the season, but only for numbered subadults/adults. The estimates calculated from numbered individuals with the LP and Bailey’s modification of LP methods at the very beginning of the season were similar to those estimated with JS and similar to the real counts in that period. For the remaining period only JS estimates are available, which showed two high peaks between the beginning of June and July (plus a few smaller peaks in spring and autumn) with estimated numbers much higher than any counts of marked individuals. In general, most numbers estimated with JS are considerably higher (> 25 times) than the real counts (of marked individuals or even of the sum of all cohorts), (compare Figures 3, 4 and 5). This could be explained by a high proportion of the population being hidden in crevices, which may lead to an unequal probability of capture. An additional explanation would be that the juveniles that were initially not marked, later grew up and were "first" recorded as newly captured individuals. This results in an artificial overestimate in summer. Thus, one of the assumptions of the JS method ("homogeneous catchability", i.e., catchability is the same for all animals at each sampling occasion) seemed to be violated by the seasonal accumulation of juveniles that could not be recorded by marking (comp. Schwarz & Arnason, 2018).

Given the high number of dotted individuals (e.g., 402 at site A) it is surprising that only a few dotted individuals were later found again and marked with a number. This means that the majority of numbered subadult/adult individuals had not been found previously. Several reasons could explain this finding. (1) The majority of juveniles died fast (e.g., unperceived in crevices inaccessible for us). (2) The majority of juveniles migrated fast out of the site. This seems to play a minor role, because at least for subadults and adults migration between sites A and B was found only for a few individuals. It can be assumed that in general movements out of the study sites were rare, albeit different dispersal behaviour of juveniles and subadults/adults cannot be ruled out. (3) Dotted individuals are only a small portion of the real number of juveniles. This seems reasonable as it would be in line with the high estimates calculated with LP and Bailey’s modification of LP methods (e.g., at site A all estimates for dotted juveniles > 240) compared to the number of dotted juveniles counted at the first day (43 at site A).

Even considering that the counted snails are only a fraction of the real population, our data reflects the development of the population with high numbers of juveniles in early spring and a drop in the middle of
May. Our recordings imply that the life cycle (the time from egg to adult stage) of *M. subcristata* is annual/biannual which is similar as found for the rock dwelling clausiliid *Albinaria caerulea* by Giokas and Mylonas (2002). Giokas et al. (2005) showed that *A. caerulea* displays seasonal patterns of activity and aestivation. Aestivation from spring to late summer was not even interrupted by rainfalls, in contrast to our study where even during the visits in the hot period in July and August snails (up to 20 individuals per site) were observed. The main reproduction period of *A. caerulea* was reported to occur in autumn. A similar seasonal regime could explain the mass appearance of juveniles of *M. subcristata* in spring as recorded in 2017.

The fact that already in the first visits in spring a few subadult/adult snails were recorded let us assume that they had survived the winter. Observations of snails maintained in our lab at the NHMW showed that individuals may survive at least two seasons (two overwintering periods), although only a few individuals lived that long. The low percentage of numbered snails found dead in the course of our field study could be explained threefold (or in combination): (1) a proportion of snails surviving the winter or even longer periods hidden in crevices, (2) a proportion of snails dying in crevices, and (3) dispersal.

**Density**

The observed maximum density of 9 individuals per m² (site A: April 30th 2017) calculated from total counts might be an underestimation. According to calculations based on the LP and Bailey's modification of LP indices they would be more than twice as high. Densities calculated from JS estimates correspond to those values at the beginning of the study but reach a maximum of 28 (site A) and 34 (site B) individuals per m². It has to be emphasized that these numbers are mean values of 16 m² areas. According to our observations the snails were not distributed randomly over the rock walls but tended to accumulate at structures and along crevices. Thus, at certain favourable places higher numbers of individuals might be found than in others. Therefore, these high maximum numbers of individuals per m² calculated in the present study from the JS estimates seem even more unrealistic. For example, for *Pyramidula* sp. densities of 25 and 9 individuals per m² were recorded in two subsequent years (Haring et al. 2018; Sattmann et al. 2019). In an overview Baur (1993) summarizes densities of adult *A. arbustorum* ranging from 0.1 to 20 adults/m².

**Dispersal**

Despite the fact that climatic conditions seem to affect activity and dispersal, which was observed mainly in rainy periods, there was variation observed at the individual level. Although the majority of individuals proved to be rather immobile (sum of MDs over the season ≤ 1.5 m), a few individuals moved around over longer distances (sum of MD up to 8.0 m). These findings are in accordance with those of Giokas & Mylonas (2004) who studied dispersal patterns and population structure of the land snail *Albinaria caerulea* during a period of 2.5 years at four sites (some of them with more and some with fewer crevices). In that study the average and minimum distances were small, i.e., 1.62 and 0.54 m respectively, with the majority of the specimens covering only short distances. Like in the present investigation only a few individuals moved over longer distances, i.e., 7.5 and 8.4 m in the study of Giokas & Mylonas (2004) and at localities with less crevices individuals tended to be more mobile. This differing individual behavior certainly deserved further investigation. It would also be interesting to assess whether dispersal activity is connected to population pressure due to increased densities. To address such questions a higher number of sites should be investigated over more than one season.

In the malacological literature there are reports of dispersal of some species. Quite a range of dispersal distances have been reported, e.g., *Theba pisana* (mean 1 m/day, up to 55 m/month; Baker 1988), *Arianta arbustorum* (0–0.45 m/day, mean of 1–5 m/3 months at different sites, mean 7–12 m/year at different sites and up to 14 m/3 months; compiled by Baur & Baur, 1993), Kleewein (1999) who studied spatial distribution and dispersal in an Austrian population of *Arianta arbustorum* showed that individuals of this species exhibit a high loyalty to their habitat. However, single individuals were found displaced up to 18 m over one season, which might have been due to passive dispersal (Kleewein, 1998). On the other hand, snails inhabiting mainly rocky substrates seem to be less mobile, e.g., *Chondrina clienta* (mean 2 m, up to 6 m/year; Baur & Baur, 1994) and *Cristataria genezarethana* (mean 0.75 m/without time specification, up to 11 m/without time specification; Heller & Dolev, 1994). Unfortunately, these dispersal measurements are not comparable among each other, because different methods and approaches were used in the various studies: recording of natural distributions (e.g., Giokas & Mylonas, 2004) and use of different spatial and temporal parameters (mean/day, min-max/month,
FIRST DATA ON POPULATION ESTIMATES AND DISPERSAL OF MONTENEGRINA SUBCRISTATA

mean/min/max/season, mean/min/max/year, movement from one observation to the next measured under different time distances). Yet, our study is in agreement with previous studies reporting comparatively low migration in rock-dwelling snails with only few individuals moving over longer distances (e.g., Kleewein, 1999; Giokas and Mylonas, 2004; Haring et al., 2018).

Temperature and Humidity
Albeit the recordings of the data loggers were hampered by technical problems, we learned a lot.

Besides the differences between study sites, we found that even within an area as small as 10–20 m² the microclimate may differ considerably. While a comparison of minimum, maximum and mean values only roughly reflects differences between sites, the profiles show oscillations over the season as well as in a daily manner in much more detail. Looking at the daily ranges it becomes apparent that site A had the highest ranges. The extreme dry and hot conditions at site C in the period from June to July might be a reason for the fact that individual numbers were extremely low at site C compared to the other two sites. Measured relative humidity of 100 % delivered at all sites for some days, while the other two sites delivered more moderate values at the same time, let us assume that in some crevices (where the loggers were deposited) condensation water and/or rain water might have accumulated and remained for longer periods than in other sites. Different exposition of certain parts of the rock face might lead to different evaporation rates.

At first sight our data suggests that the positions of the data loggers were suboptimal and should have been selected with more care to be comparable. Our aim was to put them into crevices that appeared not accessible for animals (e.g., mice), not too close to the ground, near to appropriate resting/activity sites for snails (not densely vegetated), and at places that appeared to be stable rock. Yet, the considerable differences between the humidity data recorded by the three loggers reveal microclimatic variation that might be of great relevance and might explain to some extent the irregular distribution of the snails on the rock face.

The recording of many snails in the beginning of the subsequent season (2018) after a seemingly disappearance in the foregoing autumn (data not shown), confirmed the assumption that finding probability strongly varies with environmental and/or endogenous conditions and still many individuals can remain undetected. On the other hand, the complete absence of small juveniles over two subsequent seasons (even at optimal weather conditions and even when active adults were observed) let us assume that the population might be in a critical state. Further studies would be necessary to observe if the population recovers or gets extinct and if recolonisation takes place.

Conclusion
Every rock is different. It is not possible to investigate an “ideal natural rock face” as a model. The present study was not based on a “random sampling”, but our strategy was to monitor snails at selected rock sites that appeared as suitable habitat. Yet, even a suitable area with high numbers of individuals may face a severe population decline in the next season. Methods to evaluate population sizes and densities are hampered by various factors. Real counts are underestimations and are strongly dependent on environmental circumstances. Estimations based on mark-recapture indices are depended on certain assumptions, which rarely are achievable under natural conditions. Specifically, the JS method may lead to severe overestimations due to varying catchability over the season. Nevertheless, together with further observations we conclude that there may be considerable fluctuations in population size. These might be strongly influenced by climate conditions like rain and heat. Also predation might be a factor. Dispersal ability in the studied population of M. subcristata was in general low but single individuals covered distances of at least several meters. The present data provide an orientation to assess the potential of recolonization after local extinction in Montenegrina and other rock dwelling snails.

Acknowledgements
This study is part of an OeAD-WTZ-co-operation project (Project No. ME 10/ 2016) of the University of Montenegro and the working group Alpine Land Snails of the Natural History Museum Vienna. We thank the society “Freunde des
Naturhistorischen Museums in Wien" for supporting travel costs. We are grateful to Sara Schnedl for taking the photograph of Fig. 2B.

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Supporting Information

Figure S1. Snail counts (y axis) at sites A (above) and B (below) for the three cohorts showing unmarked and recaptures separately for each visit: juveniles too small to mark, juveniles newly dotted, dotted juveniles recaptured, newly marked adult and subadult individuals, already marked adult and subadult individuals (recaptures).