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POPULATION SIZE, DENSITY, SPATIAL DISTRIBUTION AND DISPERSAL IN AN AUSTRIAN POPULATION OF THE LAND SNAIL *ARIANTA ARBUSTORUM STYRIACA* (GASTROPODA: HELICIDAE)

DORIS KLEEWEIN
Natural History Museum, Burgring 7, A-1014 Vienna, Austria
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ABSTRACT

One population of the land snail *Arianta arbustorum styriaca* (Frauenfeld, 1868), endemic in the North-eastern Alps in Austria, was investigated with regard to population size and density, spatial distribution and movement patterns of the individuals in order to obtain basic information on their population biology. The study was carried out at a site situated about 880 m above sea level in Styria, in the Gesäuse mountains over two years, using the capture-recapture technique. Population density based on the Jolly-Seber model showed variation ranging from 0.12–4.03 individuals/m^2 over the whole study period. The recapture rate after one year was generally high (up to 85% per sampling date). In most cases individuals were aggregated. The snails showed a high site fidelity; average calculated minimum areas were 0.115 m^2/day. The sum vector of all individual dispersal observations over the entire study period did not indicate a significant preference for any direction. Only during winter was a significant downhill displacement (possibly passive) detected.

INTRODUCTION

Population size, density, spatial distribution and dispersal of individuals provide basic information on population ecology, population dynamics, population genetics and evolutionary biology. Dispersal is important for the colonialization of new habitats, affects the genetic structure of a population (immigration and emigration) and influences demographic processes within the population. 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 land snail populations of the genera *Arianta* and *Cepaea* adult size, dispersal and migration of the individuals were found to be density dependent (Greenwood, 1974; Oosterhoff, 1977; Baur, 1988).

The study organism, *Arianta arbustorum* (Linnaeus, 1758) is a common and widespread helicid land snail in north-west and central Europe, living in moist habitats and reaching altitudes of up to 2700 m above sea level in the Alps (Kerney, Cameron & Jungbluth, 1983). One remarkable feature of *A. arbustorum* is its high variability in shell characters and its wide range of different habitats from lowland to alpine ones. Due to its large variation in size, shape and structure of the shell, many subspecies of *A. arbustorum* have been described (see Pfeiffer, 1848; Klemm, 1974). The difficulties and problems of characterizing a subspecies phenotypically on the basis of shell characters are discussed in detail by Nemeschkal & Kothbauer (1988, 1989); Kothbauer, Nemeschkal, Sattmann & Wawra (1991); Bisenberger (1993).

The nominate form of *A. arbustorum* has a nearly globular shell, and the umbilicus is almost closed by the reflected columellar lip. Individuals with flattened and more or less open-umbilicated shells within a limited and distinct geographical range in the North-eastern Alps are considered to be a geographical subspecies: *A. arbustorum styriaca* (Klemm, 1974; Gittenberger, 1991). Gittenberger (1991) also discussed the development and the (re)-colonization of this flat form in the Alps after late glaciations. Baminger (1997) investigated 28 populations at different localities in the Ennstaler Alpen, including the Gesäuse. Using shell-morphological characters, he clustered six populations within a very restricted area and assumed that snails of these populations belong to the *A. arbustorum 'styriaca'* group. The Geasäuse is an alpine region, with diverse mountain peaks and incisions—these spatial structures may influence the distribution of populations. One *styriaca* population in the Gesäuse was chosen to study population size, density, spatial distribution and dispersal of the snails using a capture-recapture technique over two years.

MATERIAL AND METHODS

Study site: The study site is a north-exposed mountain slope with an inclination of 30–35° in the Gesäuse mountains, Styria, Austria. The Gesäuse is part of the Ennstaler Alpen, in the East of the Nördliche Kalkalpen. The site is located approx. 3 km SE of the village Gstatterboden (14° 38′E, 47° 35′N), at an altitude of 850–880 m above sea level. The bedrock is dominated by limestone (Dachsteinkalk) (Ampferer, 1935). Snails were studied in an area of approx. 1100 m^2, which is surrounded to the south, east and west side by rock faces and rock walls. A rivulet crosses the area along with a footpath (Wasserfallweg) which is frequently used by alpinists.

Based on fourteen points placed in the study site a coordinate system with corresponding altitude was established. Some big rocks were additionally used as fix-points. Maps in the scale 1:150 of the site were drawn.

A vertical rockwall (approx. 5 m) divides the study site into two areas: area A (about 700 m^2) and area B (400 m^2). Maps of the areas A and B are given in Fig. 1(A–B), the main structures being big rocks, boulders and rock debris. Several rocks are covered with lichens, others with herbaceous vegetation and still others are bare. Between the rocks, there are patches of vegetation. The map for both areas was drawn on 4 August 1993. These data are also applied in Fig. 3(A–B) since the positions of boulders and large rocks as well as the distribution of the patchy vegetation showed no major changes in the summer seasons of 1993 and 1994.

Data collection: In this study exclusively adult individuals with a fully developed lip were considered. Each snail found for the first time was measured and marked individually. The actual position of each snail was drawn into the maps; for each sampling date a separate map was used. After marking and measuring, each snail was released exactly at the spot where it had been found.

Field work was carried out from 8 August 1993 to 30 September 1993 and from 22 May 1994 to 24 September 1994 (in all on 35 days), mainly between 10:00 and 17:00 under various weather conditions.

At the beginning of field work in 1993, I attempted to search the whole area (A and B) for *A. arbustorum styriaca* on a single day. However, the whole area was too big to accurately search, mark, measure and map the individuals. Therefore, from late September 1993 onwards, only one area was examined on a single day.

Marking: For long-term studies in the field it is necessary that marking stays permanently recognizable. Wolda (1963) marked *Cepaea nemoralis* (Linnaeus, 1758) by drilling holes into the shells and found no influence on mortality and no detectable influence on fecundity. This method was used, holes (diameter 0.8 mm) were drilled into the shells according to binary coded numbers. The snails repair their shells and through the remaining scars the individual marking is permanent. For detailed information see Kleewein (1996).

Measuring the shell characters: Shell height and shell width were measured with a vernier caliper to the nearest 0.1 mm (shell orientation according to Kerney, Cameron & Jungbluth, 1983). As a measure of shell shape, the height-width ratio was calculated. The number of whorls were counted to the nearest quarter according to Kerney, Cameron & Jungbluth (1983). The degree of umbilication was estimated after Kothbauer et al., 1991, the umbilicus width was measured by a ruler to the nearest 0.5 mm (see Baminger, 1997). On the last whorl, the intensity of the brown band was scored on a scale ranging from 0 to 3 (0 = unbanded, 1 = band faintly visible, 2 = band distinctly visible, 3 = band intensively visible).

Calculations and statistical analysis: Three different capture-recapture models were used to estimate the population size: Schnabel (1938); Schumacher & Eschmeyer (1943); Jolly-Seber (Jolly, 1965). Patterns of spatial distributions of individuals were examined by using a nearest-neighbour distance method (Clark & Evans, 1954) and the index of dispersion, Poisson distribution (see Krebs, 1989). In this paper, the 'home ranges' of *A. arbustorum styriaca* are defined as minimum areas (see Southwood, 1966) taken up by the individuals. These areas were calculated as areas within the outermost finding points of one individual within one and the same year.

For statistical analysis, the programme STATGRAPHICS Plus 5.2, serial number 4511410 was used.

RESULTS

Shell-morphological characterization: The shell characters of the individuals at the Wasserfallweg population are shown in Table 1. The depressed shell shape of 408 individuals in Area A + Area B (Ind = 0.618 ± 0.002) and the degree of umbilication (U = 8/ 6–9) makes the population evident as *A. arbustorum styriaca* (see Bisenberger, 1993; Baminger, 1997).

Population size and density: The test for equal catchability of marked individuals (Leslie, 1958) revealed that the null hypothesis (all marked individuals are recaptured with the same probability) cannot be rejected (area A: seven consecutive sampling dates, $\chi^2 = 23.23$, df = 25, $p > 0.50$; area B: eight consecutive sampling dates, $\chi^2 = 22.64$, df = 21, $p > 0.50$).

Estimates of population size and density according to three different capture-recapture models (Schnabel, 1938; Schumacher & Eschmeyer, 1943; Jolly, 1965) are shown in Table 2. The population size estimation based on the model Jolly (1965) yields wide confidence limits in Area A and Area B. In average (1993–1994) low population size (109 individuals) was estimated in area B although a total of 210 individuals were marked in this area. The population size estimations (model Jolly, 1965) for each sampling date can be seen in Fig. 2(A–B).

Spatial distribution of the individuals: Examples of the spatial distributions of adult *A. arbustorum styriaca* at the Wasserfallweg can be seen in Fig. 1(A–B). Two models were used to test the spatial distributions statistically (Table 3). According to the nearest-neighbour distance method (Clark & Evans, 1954), adult *A. arbustorum styriaca* in both areas were aggregated on 70.4% of the tested dates (n = 27). Tested with the Poisson distribution, the snails in both areas occurred aggregated on 92.6% of the tested dates (n = 27).

'Home ranges': Fig. 3(A–B) shows examples of 'home ranges' of some individuals of adult *A. arbustorum styriaca* in area A (Fig. 3A) and area B (Fig. 3B). The calculated 'home ranges' are shown in Fig. 4 as a frequency histogram of the 'home ranges'/individual and per day in both areas. The distribution is logarithmic normal (normal probability plot, Chi square test: $\chi^2 = 4.349$, df = 4, p = 0.361). The calculated 'home ranges' in the areas A and B ranged from 0.001 to 1.064 m^2/day (Mean = 0.115, S.E. = 0.03, n = 50). No correlation between the 'home ranges'/individual and time interval (Pearson correlation, two-tailed: r = 0.197, p = 0.171, n = 50) was found. Also, no correlation between the logarithm of the 'home ranges'/individual and per day and the logarithm of shell width was found (Pearson correlation, two-tailed: r = 0.151, p = 0.295, n = 50). Thus, 'home range' size was not affected by the size of the snails.

Table 1. Shell characters of adult *A. arbustorum styriaca* in area A (n = 204) and area B (n = 204). **H** = shell height (mm), **W** = shell width (mm), **Ind** = H/W-shell shape, **Wh** = number of whorls, **U** = degree of umbilication (0: closed umbilicus, 1–10: 10%–100% open umbilicus), **UW** = umbilicus width (mm), **Ban** = banding (0: unbanded, 1–3: intensity of the brown band).

t-test (df = 406) for **H**, **W** and **Ind** (Mean ± Standard Error), the lower and upper quartile is given as an equivalent for the confidence limit of the median for **Wh**, **U**, **UW** and **Ban.** ns = no significant difference.

shell character	area A	area B	t-test, p
H	14.27 ± 0.07	14.14 ± 0.07	t = 1.292, p > 0.19; ns
W	23.02 ± 0.08	23.00 ± 0.09	t = 0.148, p > 0.80; ns
Ind	0.621 ± 0.002	0.614 ± 0.002	t = 1.706, p > 0.08; ns
Wh	5.25/ 5.25–5.25	5.25/ 5.125–5.25	ns
U	8/ 6–9	8/ 5–9	ns
UW	3/ 3–3.5	3/ 3–3.5	ns
Ban	3/ 3–3	3/ 3–3	ns

Table 2. Estimates of population size and density (individuals/m^2) of adult *A. arbustorum styriaca* in area A (approx. 700 m^2) and area B (approx. 400 m^2) by three different capture-recapture models. The confidence limits (95%) are given in parentheses.

model	area A	area B	area A + area B
Schnabel (1938)			
population size	730 (648–836)	242 (209–287)	972
density	1.04 (0.93–1.20)	0.61 (0.52–0.72)	0.88
Schumacher & Eschmeyer (1943)			
population size	712 (634–811)	271 (231–328)	983
density	1.02 (0.91–1.16)	0.68 (0.58–0.82)	0.89
Jolly (1965)			
population size	655 (186–2821)	109 (47–237)	764
density	0.94 (0.27–4.03)	0.27 (0.12–0.59)	0.69

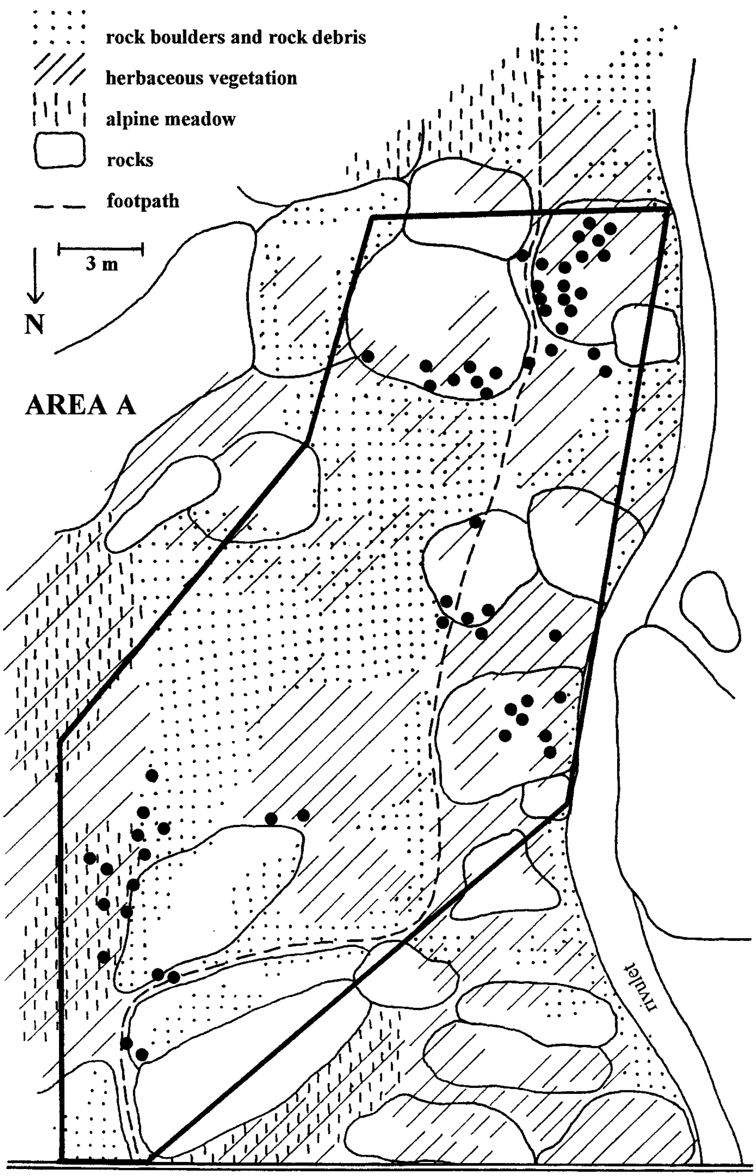

Figure 1 (A–B): Characterization of the areas A and B and examples of the spatial distribution of adult *A. arbustorum styriaca* in there.

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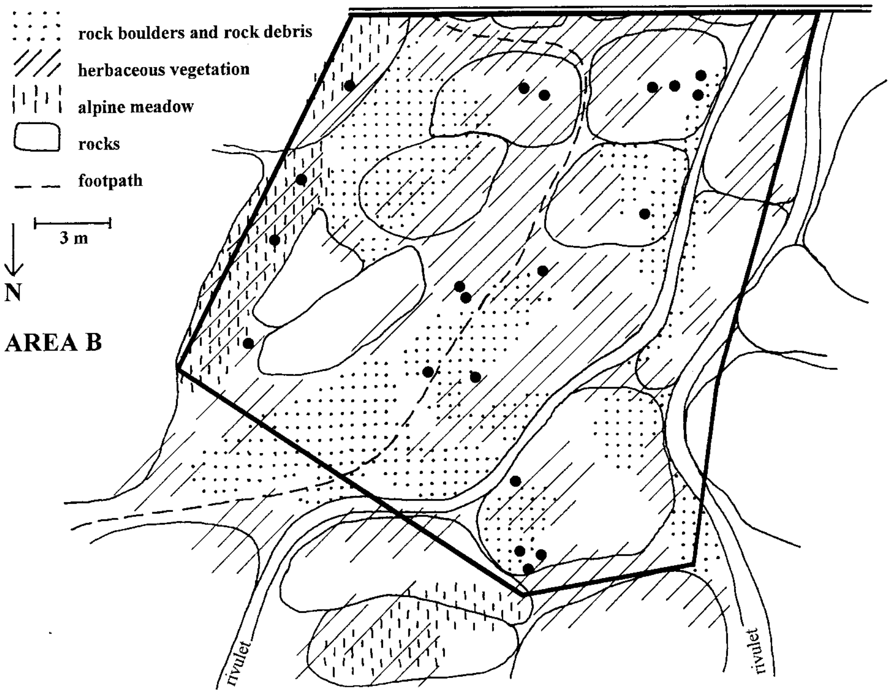
N = north direction and fall line, the double line indicates that area A and area B are bordering, but separated by an approx. 5 m difference in altitude. Both maps were drawn on 04 August 1993. The framed area was scanned on one sampling date; one point represents one individual.

Fig. 1A: area A on 21 August 1993 (n = 60). Fig. 1B: area B on 22 August 1993 (n = 20).



Dispersal: Seven individuals moved from one area to the other. Two of them were first found in area A and later in the same year recaptured in area B, and two vice versa. Three individuals were found in area A in 1993 and recaptured in area B in 1994, which is downhill over the winter season. During both investigation periods the mean distances moved per individual and per day ranged from 0.001 to 5.475 m (Mean = 0.176, S. D. = 0.601, n = 199) in the areas A and B. No correlation between the mean distances per individual and per day and the shell width was found (Pearson correlation, two-tailed: r = 0.053, p = 0.455, n = 199). Bigger (shell width) adults of *A. arbustorum styriaca* did not move greater distances than smaller ones.

The high site fidelity of adult *A. arbustorum styriaca* at the Wasserfallweg is also reflected in the very small dispersal vectors (Fig. 5). The vectors represent the mean vectors per day of the individual dispersal vectors; the individual dispersal vector was generated by averaging all the distances between two consecutive findings of one individual. The confidence limits (95%) cut the zero-point of the coordinate system in vector 1 (sum vector), vector 2 ('summer dispersal') in all four cardinal points, and in vector 3 ('winter dispersal') in the east, west and south direction; therefore, in these directions, no significant dispersal of the population from the zero-point occurred. Only in vector 3, in the north direction (fall line, downhill) a significant displacement of the population from the zero-point took place.

DISCUSSION

In the study site at the Wasserfallweg there are no significant differences in any of the shell parameters between the individuals in area A and area B. Therefore, the rockwall that separates the areas A and B is not a barrier with respect to differentiation in shell characters. Limited dispersal, caused by natural or artificial structures might lead to differentiation of *Arianta*-populations. Baur & Baur (1990) mentioned that roads and tracks may act as dispersal barrier for *A. arbustorum*, whereas an overgrown path did not influence the movement of the snails.

Population size estimations at the Wasserfallweg showed no significant differences between the three models, even though the models make different assumptions. Schnabel (1938)

AREA A

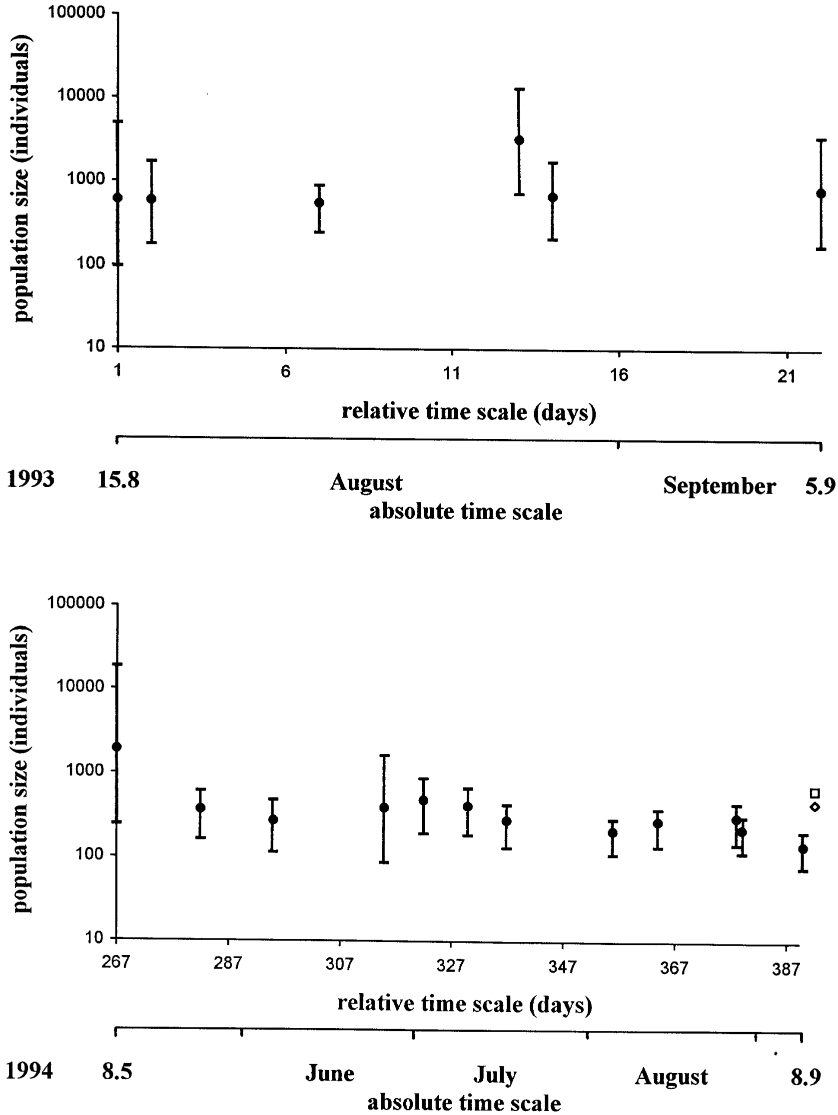
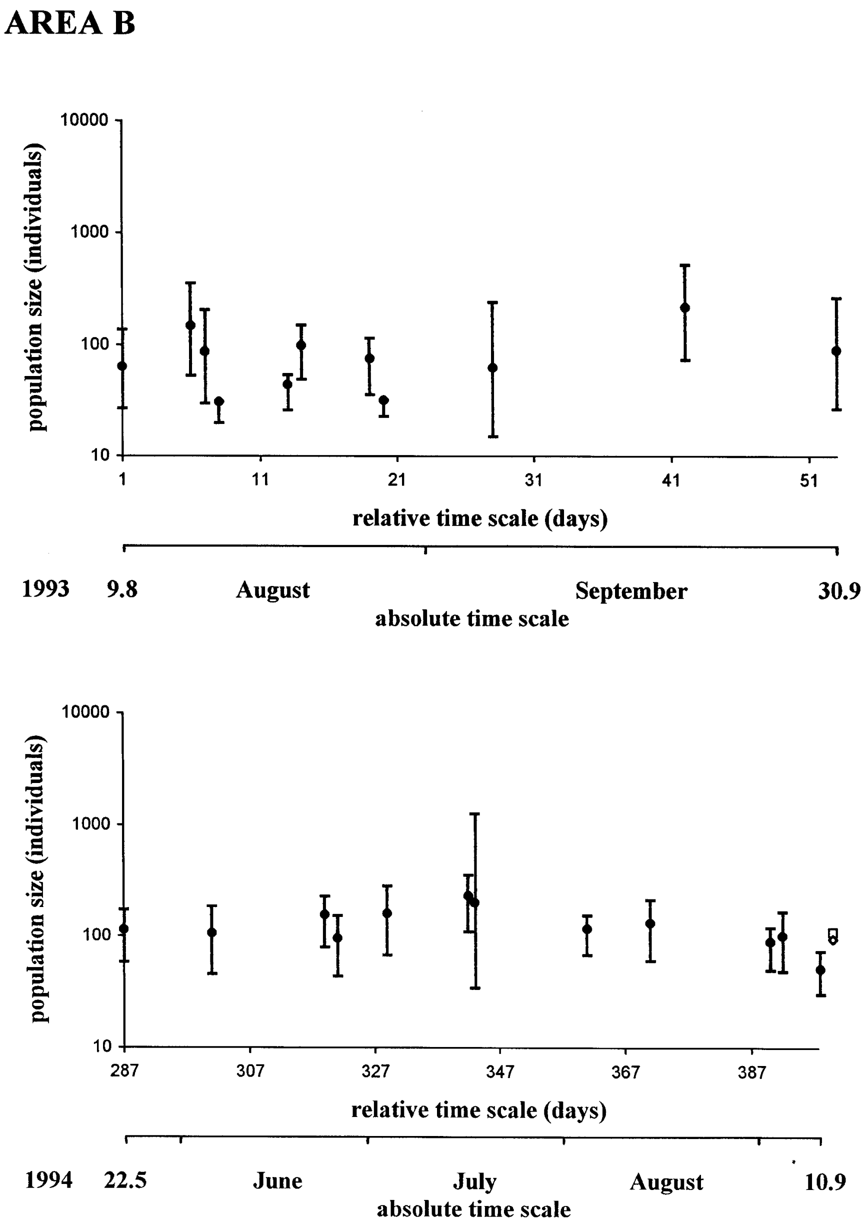


Figure 2 (A–B): Estimations of the population size (●) and 95% confidence limit (—) just before each sampling date (based on the capture-recapture model Jolly, 1965) in area A (Fig. 2A) and area B (Fig. 2B).

The relative time scale (in days) starts with the second sampling date. Note that the y-axis is in a logarithmic scale. □: arithmetic mean of the population estimations over the whole period: ◇: geometric mean of the population estimations over the whole period.



and Schumacher & Eschmeyer (1943) treat a population as closed, whereas Jolly (1965) assumes an open population (during an investigation, the size of a population is changing due to births, deaths, immigrations and emigrations). The population of *A. arbustorum styriaca* at the Wasserfallweg can be considered as open in the sense of Jolly (1965) during the investigations (2 years), because *A. arbustorum styriaca* reaches adulthood from subadult (4-4,5 whorls) after one hibernation (in laboratory Baumgartner, 1997) and Andreassen (1981) suggested an annual survival rate for adult *A. arbustorum* in Norway of between 33% and 50%.

In area A, the population size estimations

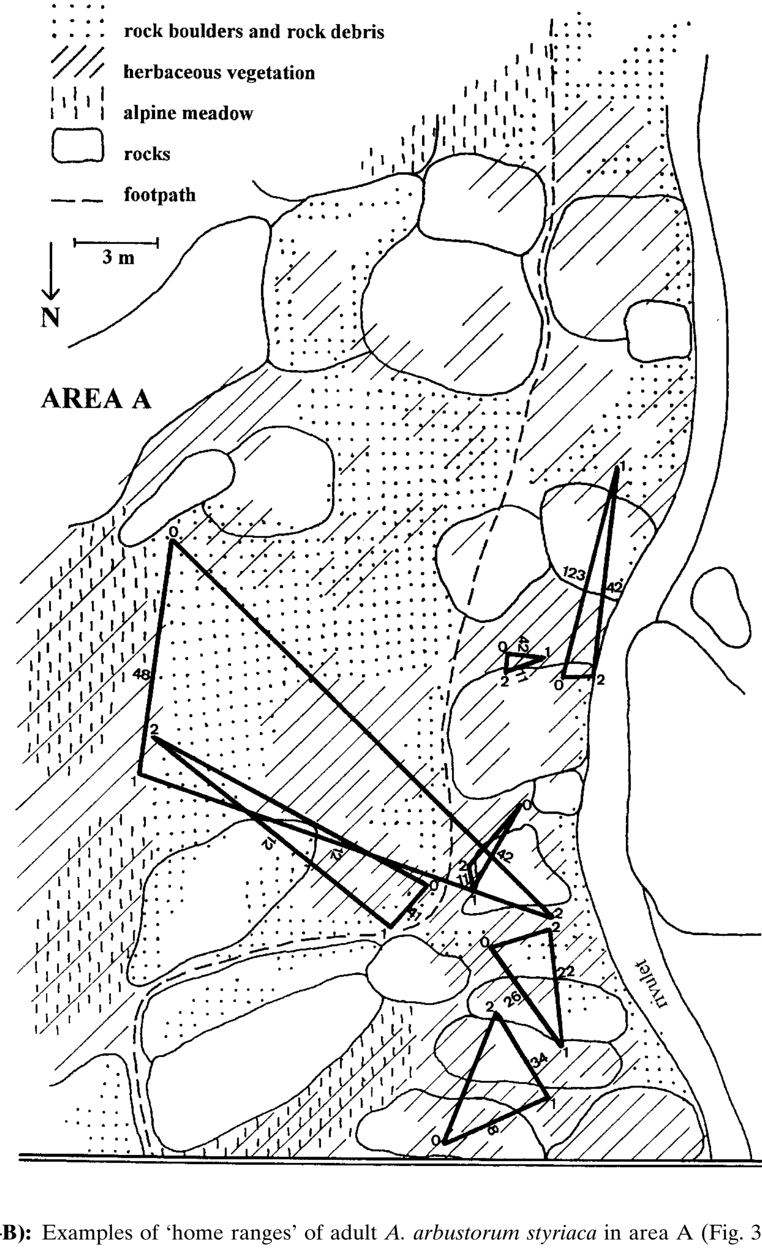
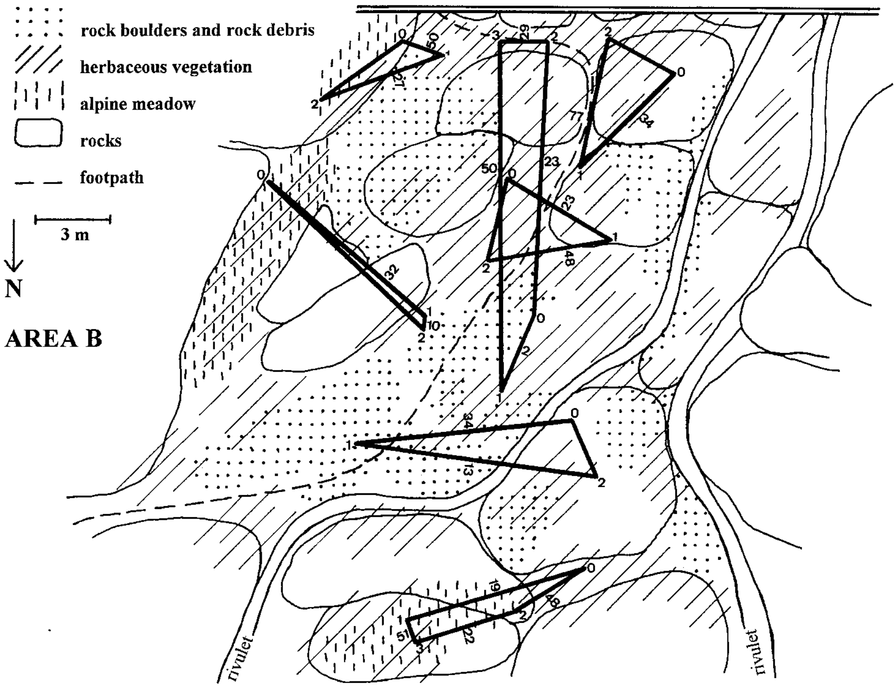


Figure 3 (A–B): Examples of ‘home ranges’ of adult *A. arbustorum styriaca* in area A (Fig. 3A) and area B (Fig. 3B).

The numbers at the corners mark the sequence of the finding points of one individual, i.e.: 0 = capture, 1 = first recapture, 2 = second recapture etc. The numbers beside the lines represent the time intervals (in days) between the two finding points at the corners.



and the confidence limits become balanced with increasing time (Fig. 2A), whereas in area B no such balancing is evident (Fig. 2B). Low population estimations were obtained on dates when the proportion of recaptures was high. On 28 August 1993, for example, in area B only one individual was found, and it had already been marked. This was in the early phase of the field work, before I treated area A and area B as separate. In 1994 (Fig. 2B), however, in area B no explanation can be given by varying the method, and the estimations fluctuate too. In area B, marking was apparently very 'dense' because the proportion of recaptures in 1994 was high which points to high site fidelity of the individuals in the Wasserfallweg population. Population size can be obtained either by directly counting the individuals or by applying capture-recapture techniques. Direct counting underestimates the true population size because the finding proportion depends on climatic and vegetation factors and also on the behavioural patterns of the snails themselves (Cain & Currey, 1968; Williamson, Cameron & Carter, 1977; Baur, 1984, 1986). Many authors have dealt with the problems of biased results by estimating the population size of snails by capture-recapture techniques (see Bailey, 1951; Southwood, 1966; Greenwood, 1974; Cameron & Williamson, 1977; Begon, 1979).

The individuals at the Wasserfallweg mostly showed aggregated distribution. In one part in area A, where only rock boulders and rock debris and no vegetation occurred, *A. arbustorum styriaca* was rarely found over the two summer seasons; this site appeared to be unfavourable for the snails. Aggregated distribution patterns of dispersion in *A. arbustorum* was also found by Andreassen (1981); Ledergerber, Baminger, Bisenberger, Kleewein, Sattmann & Baur (1997), different aggregation patterns in different age classes of *A. arbustorum* were found by Baur (1984) and that aggregation is highest on dry days in summer (Baur, 1986). Factors favouring an aggregated pattern may include small-scale differences in micro-climate, habitat heterogeneity, the probability of finding a mating partner and the patchy distribution of food.

Adult individuals of *A. arbustorum styriaca* at the Wasserfallweg apparently have restricted 'home ranges' (Fig. 4), whose size is not affected by shell size. The 'home ranges' of the individuals may represent their demand for a

Table 3. Analysis of the spatial distributions of adult *A. arbustorum styriaca* in the areas A and B by a nearest-neighbour distance method (Clark & Evans, 1954) and the index of dispersion, Poisson distribution (see Krebs, 1989). The calculations were made only for those days on which at least 20 individuals were found.

Nearest-neighbour distance method : R = Index of aggregation, z = standard normal deviate. If R = 1: random spatial pattern (ra), if R < 1: aggregated spatial pattern (a), if R approaches an upper limit around 2.15: regular spatial pattern (re).

Test for significance (95%): if |z| is less than 1.96: random spatial pattern.

Poisson distribution: I = Index of dispersion. If I is much larger than 1.0: aggregated spatial pattern (a), if I is close to zero: regular spatial pattern. Test for significance (95%): χ^2 0.975 < observed χ^2 < χ^2 0.025: random spatial pattern (ra), df = degrees of freedom.

			nearest-neighbour distance method			index of dispersion, Poisson distribution			
date	n	area	R	z	spatial distribution	I	df	χ^2 observed	spatial distribution
08/08/1993	21	B	0.728	−2.385	a	2.22	14	31.14	a
14/08/1993	22	A	1.264	2.369	re	5.60	18	100.64	a
15/08/1993	29	A	1.490	5.046	re	4.79	12	57.52	a
16/08/1993	40	A	1.000	0.011	ra	3.73	15	56.00	a
21/08/1993	60	A	0.638	−5.368	a	6.18	18	117.33	a
22/08/1993	20	B	0.881	−1.020	ra	19.84	18	396.70	a
27/08/1993	29	A	0.655	−3.558	a	4.99	14	69.80	a
28/08/1993	21	A	0.701	−2.617	a	2.08	16	33.24	a
22/05/1994	26	B	0.560	−4.290	a	4.25	12	51.00	a
23/05/1994	42	A	0.604	−4.910	a	7.93	9	71.34	a
05/06/1994	21	A	0.593	−3.569	a	2.85	13	37.00	a
23/06/1994	32	B	0.574	−4.613	a	2.14	12	25.69	a
02/07/1994	33	A	0.252	−8.217	a	5.23	11	57.55	a
10/07/1994	41	A	0.545	−5.571	a	3.11	14	43.51	a
16/07/1994	36	B	0.915	−0.978	ra	2.03	24	46.67	a
17/07/1994	34	A	0.519	−5.369	a	2.67	18	45.41	a
04/08/1994	34	B	0.570	−4.794	a	4.04	18	68.71	a
05/08/1994	35	A	0.685	−3.562	a	15.57	9	140.14	a
13/08/1994	34	A	0.896	−1.164	ra	3.59	13	46.71	a
27/08/1994	34	A	0.406	−6.624	a	6.22	12	74.59	a
28/08/1994	39	A	0.466	−6.378	a	4.22	14	59.08	a
02/09/1994	24	B	0.715	−2.666	a	3.38	15	50.67	a
04/09/1994	20	B	1.058	0.500	ra	2.02	13	26.20	ra
08/09/1994	39	A	0.480	−6.212	a	2.41	14	33.69	a
10/09/1994	21	B	0.878	−1.070	ra	1.80	15	27.00	ra
16/09/1994	37	A	0.441	−6.508	a	6.14	10	61.41	a
24/09/1994	20	B	0.632	−3.145	a	2.32	14	32.50	a

certain area over a certain time. Small 'home ranges' indicate strong site fidelity; for example that the individuals find food, resting places, mating partners and places for egg deposition in a relative restricted area.

Mean distances moved were similar as those in other studies on *A. arbustorum* (Baur, 1984, 1986; Baur & Baur 1990, 1993). During 'winter period' (from 30 September 1993 to 08 May 1994) downhill displacements of individuals were recorded. These data do not allow distinction between active dispersal and passive displacements. Passive ones may occur at the Wasserfallweg (i.e. downhill by strong water effects, avalanches or falling stones). Baur (1984, 1986) mentioned individuals of *A. arbustorum* with globular shells rolling down on snow-covered slopes and snowfields. Eventually the individuals compensate the (passive) downhill displacement over winter with uphill movement in spring, after hibernation. Baur (1984, 1986) noted a tendency of *A. arbustorum* to move uphill in summer and autumn, and Baur & Gosteli (1986) pointed out that *A. arbustorum* shows negative geotactic orientation behaviour. Most recently, Baur, Leder-

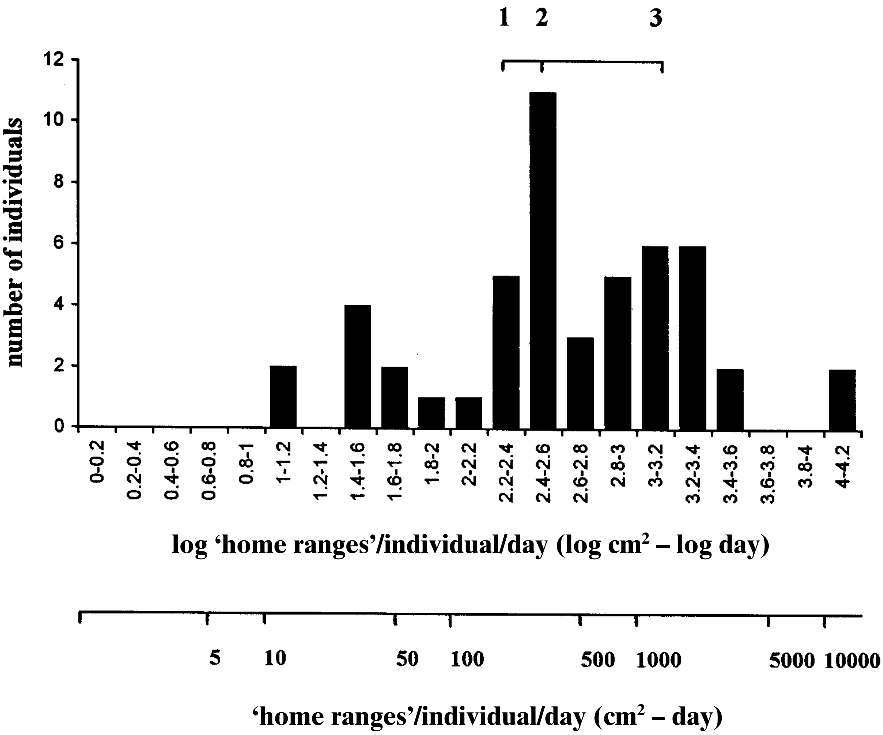


Figure 4: Frequency histogram of the 'home ranges' per individual and per day of adult *A. arbustorum styriaca* in the areas A and B.

The 'home ranges' were calculated as areas within the outermost finding points of one individual in one and the same year, then divided by the entire period between the capture and the last recapture within that year. In the calculations only individuals with more than one recapture are included (n = 50).
1 = lower quartile, 2 = median, 3 = upper qaurtile

gerber & Kothbauer (1997) showed that *Arianta chamaeleon* (Pfeiffer, 1842), characterized by even more flattened shells than *A. arbustorum styriaca*, has a lower probability of rolling downhill on a snow-covered slope than *A. arbustorum* with globular shells. A lower percentage of *A. chamaeleon* rolled long distances compared with *A. arbustorum*. Individuals with flattened shells may therefore show a more pronounced site fidelity than individuals with globular shells.

The population at the Wasserfallweg is one of the few ones with individuals which show the extreme flat and wide open umbilicated shells. In the near neighbourhood (see Baminger, 1997) there exist no populations with individuals with globular and not umbilicated shells. *A. arbustorum styriaca* at the Wasserfallweg is spatially separated. The individuals show low dispersal and small 'home ranges', they can be regarded as showing local site fidelity. Additionally to other works on *A. arbustorum* in the Gesäuse (Baminger, 1997; Baumgartner 1997) these date could point to the possibility that a process of species separation might take place.

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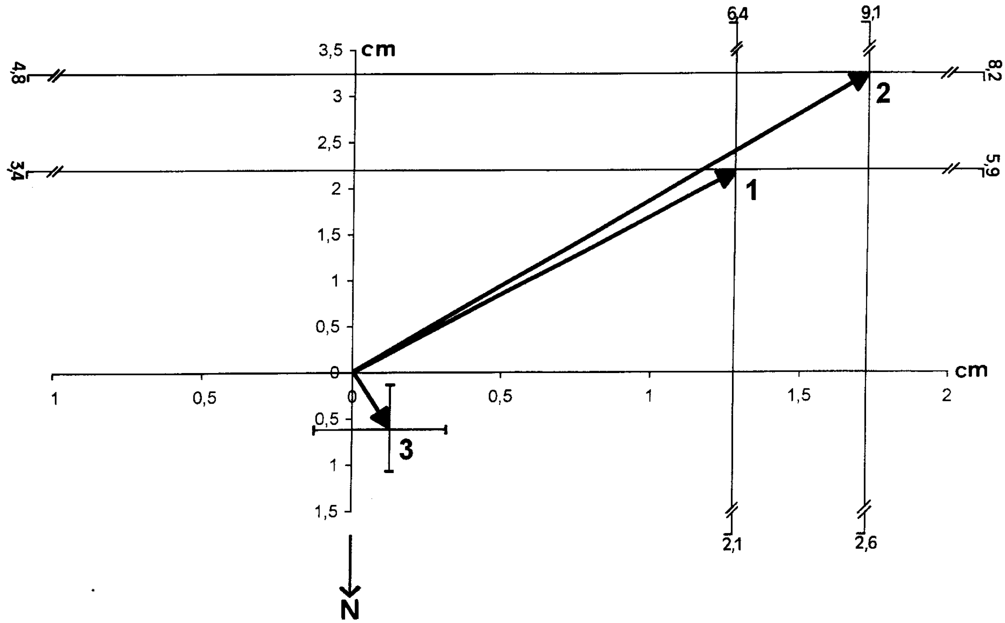

Figure 5: Mean vectors per day of the individual dispersal vectors of adult *A. arbustorum styriaca* in the areas A and B.

The individual dispersal vector was generated by averaging all the distances between two consecutive findings of one individual.

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N = north direction and fall line.
Vector 1: sum vector: mean vector per day over all individual dispersal observations (n = 282).
Vector 2: 'summer dispersal': mean vector per day of the individual dispersal observations in the periods from 08 August 1993 to 30 September 1993 and from 08 May 1994 to 10 September 1994 (n = 205).
Vector 3: 'winter dispersal': mean vector per day of the individual dispersal observations in the period from 30 September 1993 to 08 May 1994 (n = 77).
For each mean vector the confidence interval (95%) is given by Mean ± t × S. E.

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