

DIFFERENCES IN RESTING-SITE PREFERENCE IN TWO COEXISTING LAND SNAILS, *ARIANTA ARBUSTORUM* AND *ARIANTA CHAMAELEON* (HELICIDAE), ON ALPINE SLOPES

STEPHAN LEDERGERBER¹, HELMUT BAMINGER², AGNES BISENBERGER², DORIS KLEWEIN², HELMUT SATTMANN³ and BRUNO BAUR¹

¹ Conservation Biology Research Group (NLU), University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland. ² Institute of Zoology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria. ³ Natural History Museum, Burgring 7, A-1014 Vienna, Austria
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ABSTRACT

Resting-site preference and patterns of spatial distribution were examined in the sympatric land snails *Arianta arbustorum* and *A. chamaeleon* on two opposite slopes in the south-eastern Alps, Austria. The two slopes did not differ in proportion of *A. arbustorum* and *A. chamaeleon* (74.4% vs. 25.6% on the NNE-exposed slope and 68.3% vs. 31.7% on the SSW-exposed slope). Individuals of both species showed aggregated dispersion patterns. The nearest-neighbour method indicated that in both species snail aggregations predominantly consisted either of *A. arbustorum* or *A. chamaeleon* on the NNE-exposed slope with a mosaic of rocks and distinct patches of different plants. On the SSW-exposed slope, which was less variable in vegetation cover, snail aggregations consisted of conspecific and hetero-specific individuals. Juvenile and adult *A. arbustorum* preferred to rest attached to leaves of *Adenostyles alliariae*, but avoided rock surfaces and patches of grass on the NNE-exposed slope. In contrast, juvenile and adult *A. chamaeleon* preferentially rested on rock surfaces, and also avoided grass patches. Juvenile and adult *A. chamaeleon* did not differ in resting-site preference, whereas small differences in resting sites were observed between juvenile and adult *A. arbustorum*. Differences in resting-site preference is one way of niche differentiation which may allow individuals of the two *Arianta* species to coexist.

INTRODUCTION

Niche differentiation is often the basis for the coexistence of competitors (MacArthur & Levins, 1967; Roughgarden, 1979). Differential resource utilization can be expressed in a number of ways. Species may differ in their food choice and/or microhabitat use. Further-

more, the resources utilized by ecologically similar species can be separated in time or in space. Among gastropods, differential habitat selection has been demonstrated in coexisting *Partula* species on Moorea (Murray, Johnson & Clarke, 1982). Temporal differences in resource utilization have been found in *Cepaea nemoralis* (L.) and *C. hortensis* (Müller), which differ in their period of maximum activity (Cameron, 1970). The land snail *Mesodon thyroidus* (Say) shows less restricted weather requirements for activity than the sympatric *Triodopsis albolabris* (Say) (Emberton, 1981). A separation of food resources has been demonstrated in the coexisting rock-dwelling land snails *Chondrina clienta* (Westerlund) and *Balea perversa* (L.) (Fröberg, Baur & Baur, 1993; Baur, Baur & Fröberg, 1994), and in hydroid-eating nudibranchs (Lambert, 1991). However, in many cases ecologically similar species can only coexist when they differ in more than one niche dimension. For example, specific differences in food habits and substrate choice allow the coexistence of several *Conus* species (Kohn, 1959, 1968; Kohn & Nybakken, 1975).

The aim of the present study was to examine the spatial distribution and resting-site preference of *Arianta arbustorum* (Linnaeus, 1758) and *A. chamaeleon* (L. Pfeiffer, 1842). Both species usually occur allopatrically, but coexist in some alpine sites in southern Austria (Klemm, 1974; H. Sattmann, unpubl. data). Intraspecific density effects on juvenile growth, adult shell size, clutch size and incidence of egg cannibalism have been shown in *A. arbustorum* (Reichardt *et al.*, 1985; Baur, 1988). However, very little information on the ecology of

A. chamaeleon is available. In this paper we address the following questions: (1) do individuals of *A. arbustorum* and *A. chamaeleon* differ in their spatial distribution when they occur in the same habitat? (2) Are there species-specific resting-site preferences? And (3) do juveniles and adults of the same species differ in their resting-site preferences?

MATERIALS AND METHODS

Arianta arbustorum is common in moist habitats in north-western and central Europe (Kerney, Cameron & Jungbluth, 1983), occurring at altitudes of up to 2700 m a.s.l. in the Alps (Baur & Raboud, 1988). *Arianta chamaeleon* lives in the south-eastern Alps (Kerney *et al.*, 1983). Snails of both species have determinate growth, but differ in banding characteristics of the shell and in shell shape (ratio shell height/shell breadth) (Bisenberger, 1993). In the populations examined in this study, *A. arbustorum* has a more globular shell (shell shape 0.80), whereas *A. chamaeleon* has a flattened, nearly discoidal shell (shell shape 0.57; Baur, Ledergerber & Kothbauer, 1997).

The resting sites of *A. arbustorum* and *A. chamaeleon* were recorded in an alpine meadow partly covered with calcareous rocks and rock debris near Lake Wolay at an elevation of 1970 m a.s.l. in south-western Carinthia, Austria (46°37'N, 12°52'E). Two plots were established on the opposite slopes of a small valley. Plot A was a 5-m wide and 38-m long strip that ranged from the bottom of the valley to the middle part of the NNE-exposed slope (range of inclination: 0–30°). Plot B was situated on a SSW-exposed slope (inclination: 55°). It measured 6 × 12 m and was 10 m apart from plot A separated by a track. A part of plot B is covered with rock plates and rock walls. Plot B was smaller than plot A because adjacent rock walls made any field work dangerous.

In both plots a grid of 1 m² units was set up using lines. The plots were carefully searched for *A. arbustorum* and *A. chamaeleon* between 10 a.m. and 1 p.m. by eight persons on 25 July 1995 (plot B) and by 11 persons on 26 July 1995 (plot A). On both days the weather was fine (sunshine with an air temperature ranging from 14.6 to 19.0°C). The snails were inactive and therefore the positions recorded represent their daytime resting sites. For each snail found we recorded the species, age class (juveniles were individuals without a reflected shell lip and adults individuals with a reflected lip), and the type of habitat (rock or vegetation) in which the resting animal was found (see below). The position of each snail was recorded by measuring the distances to the nearest two grid lines. Cartesian coordinates were calculated on the basis of these data. The snails remained at their original positions. In plot A one person mapped the spatial distribution of rocks and stones

and different types of vegetation. In plot B, no distinct patches of different vegetation were recognizable. Therefore, we only recorded whether the snails rested on rocky surfaces or in the vegetation in plot B.

RESULTS

Proportion of rocks and vegetation in the plots

The two plots did not differ in the percentage of area covered either by rocks or vegetation (Fig. 1; plot A: rocks 40.3%, vegetation 59.7%; plot B: rocks 39.2%, vegetation 60.8%; $\chi^2 = 0.03$, d.f. = 1, $P > 0.9$). Table 1 gives a summary of the percentage cover of the different plant species in plot A.

Number and spatial distribution of resting snails

A total of 531 snails were found in plot A (*A. arbustorum*: 74.4%; *A. chamaeleon*: 25.6%; Table 1). In plot B, 139 snails were recorded (*A. arbustorum*: 68.3%; *A. chamaeleon*: 31.7%). The two plots did not differ in proportion of *A. arbustorum* and *A. chamaeleon* ($\chi^2 = 2.05$, d.f. = 1, $P > 0.15$; Table 2). Furthermore, the two plots did not differ in proportion of juvenile and adult *A. chamaeleon* ($\chi^2 = 0.01$, d.f. = 1, $P > 0.9$; Table 2). However, significantly more adult *A. arbustorum* were found in plot A than in plot B ($\chi^2 = 11.82$, d.f. = 1, $P < 0.001$; Table 2).

Juveniles and adults of both species were significantly aggregated, except adult *A. chamaeleon* in plot B (nearest-neighbour method of Clark & Evans (1954); Table 2 and Fig. 1). In plot A, the nearest neighbour was more frequently a conspecific than expected under the assumption that the snails were neighbours in the same proportion as *A. arbustorum* and *A. chamaeleon* occurred in the plot ($\chi^2 = 139.48$, d.f. = 1, $P < 0.0001$). This indicates that snail aggregations mainly consisted of conspecifics in plot A which was a mosaic of rocks and patches of different plants (Fig. 1a). In plot B, however, the nearest neighbour was either a conspecific or an individual of the other species, with frequencies corresponding to the proportions in which they occurred in the area ($\chi^2 = 1.25$, d.f. = 1, $P > 0.25$). In contrast to plot A, plot B contained no distinct patches of different plants (Fig. 1b).

Table 1. Cover of rocks and different plant species and number (%) of juvenile and adult *A. arbustorum* and *A. chamaeleon* found in patches of different vegetation in plot A.

Substrate and plant species	% cover	Number (%) of resting snails			
		<i>A. arbustorum</i>		<i>A. chamaeleon</i>	
		juveniles	adults	juveniles	adults
Rocks	40.3	37 (16.2)	10 (6.0)	57 (57.0)	20 (55.6)
Grass and herbs	30.8	38 (16.7)	19 (11.4)	15 (15.0)	5 (13.9)
<i>Adenostyles alliariae</i>	24.7	129 (56.6)	121 (72.5)	22 (22.0)	8 (22.2)
<i>Geranium sanguineum</i>	1.6	6 (2.6)	5 (3.0)	1 (1.0)	1 (2.8)
<i>Cirsium spirasissimum</i>	1.3	2 (0.9)	0 (0.0)	3 (3.0)	2 (5.6)
<i>Salix</i> sp.	0.7	5 (2.2)	2 (1.2)	1 (1.0)	0 (0.0)
<i>Veratrum album</i>	0.4	10 (4.4)	7 (4.2)	0 (0.0)	0 (0.0)
<i>Aconitum napellus</i>	0.1	0 (0.0)	3 (1.8)	0 (0.0)	0 (0.0)
<i>Peucedanum</i> sp.	0.1	1 (0.4)	0 (0.0)	1 (1.0)	0 (0.0)

Table 2. Number of snails, density and pattern of spatial distribution of *A. arbustorum* and *A. chamaeleon* found on the opposite slopes of an alpine valley in south-western Carinthia, Austria. Patterns of spatial distribution were analysed using the distance-to-nearest-neighbour method of Clark & Evans (1954). R-values < 1 indicate a tendency towards aggregation. Significance levels: * P < 0.02; ** P < 0.01; *** P < 0.001.

Species	Age class	Number of snails (%)	Density (individuals/m ²)	Dispersion coefficient R
NNE-exposed slope (plot A):				
<i>A. arbustorum</i>	Juveniles	228 (57.7)	1.20	0.59 ***
	Adults	167 (42.3)	0.88	0.55 ***
	Juveniles + adults	395 (100.0)	2.08	0.58 ***
<i>A. chamaeleon</i>	Juveniles	100 (73.5)	0.53	0.78 ***
	Adults	36 (26.5)	0.19	0.80 ***
	Juveniles + adults	136 (100.0)	0.72	0.75 ***
SSW-exposed slope (plot B):				
<i>A. arbustorum</i>	Juveniles	73 (76.8)	1.01	0.67 ***
	Adults	22 (23.2)	0.31	0.50 ***
	Juveniles + adults	95 (100.0)	1.32	0.61 ***
<i>A. chamaeleon</i>	Juveniles	32 (72.7)	0.44	0.81 **
	Adults	12 (27.3)	0.17	1.15 N.S.
	Juveniles + adults	44 (100.0)	0.61	0.80 *

Resting-site preferences on the NNE-exposed slope (plot A)

The position of each snail is shown in relation to rocks and patches of different vegetation on the NNE-exposed slope (plot A) in Fig. 1a. The percentages of *A. arbustorum* and *A. chamaeleon* found attached to rocks or in patches of different vegetation are presented in relation to the percentage cover of the plants and rocks in Fig. 2. In both snail species, the frequencies of different resting sites chosen deviated from the proportion of the occur-

rence of rocks and different plant species (*A. arbustorum*: $\chi^2 = 165.39$, d.f. = 5, $P < 0.0001$; *A. chamaeleon*: $\chi^2 = 12.32$, d.f. = 3, $P = 0.006$). Individuals of *A. arbustorum* preferred to rest attached to leaves of *Adenostyles*, but were scarce on rock surfaces and in patches of grass (Table 1). In contrast, individuals of *A. chamaeleon* were mainly found on rock surfaces, but were also scarce in grass patches.

Comparing the two species, juveniles and adults of *A. arbustorum* occurred more frequently on *Adenostyles* than juveniles and adults of *A. chamaeleon*, which in turn rested

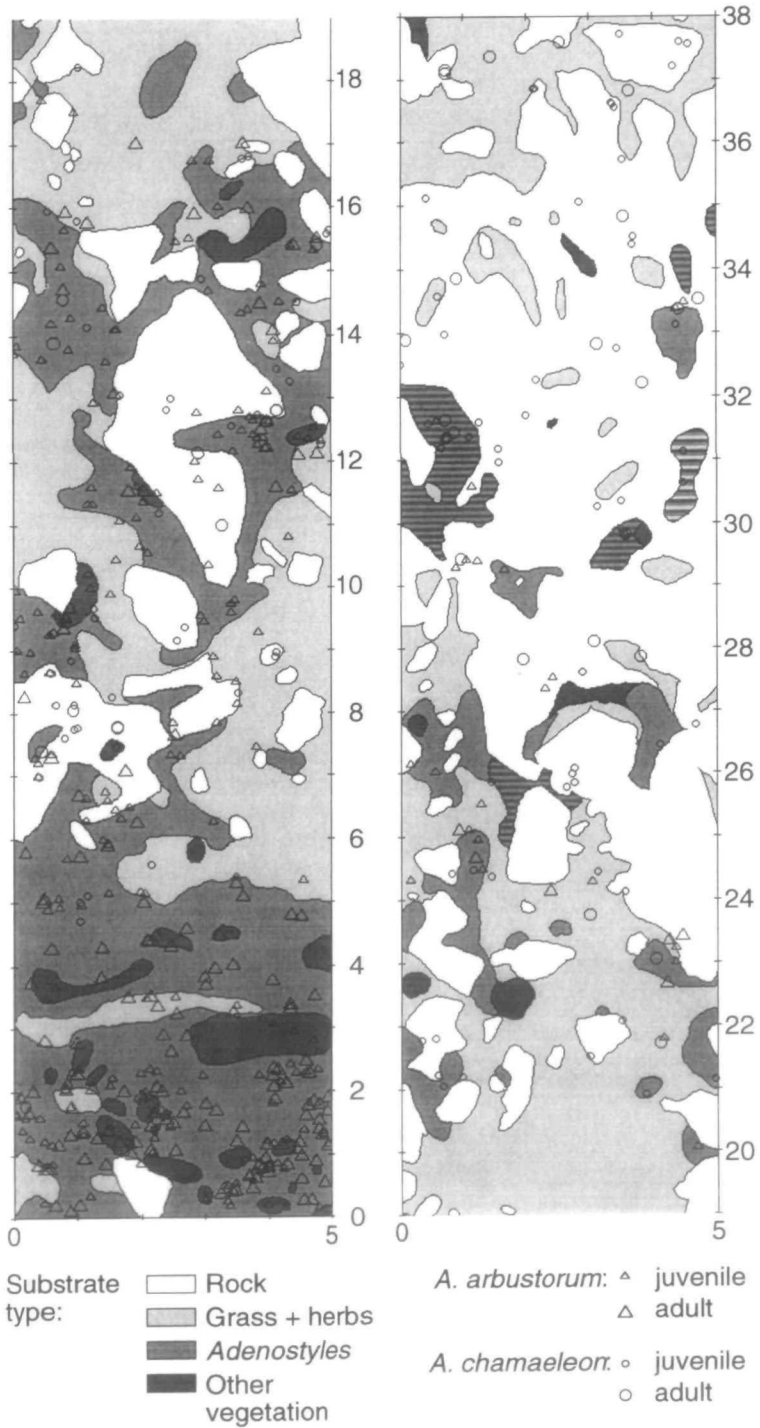


Figure 1. Maps showing the spatial distribution of rock surface and patches of different plant species and the positions of *A. arbustorum* and *A. chamaeleon* in (a) plot A, and (b) plot B.

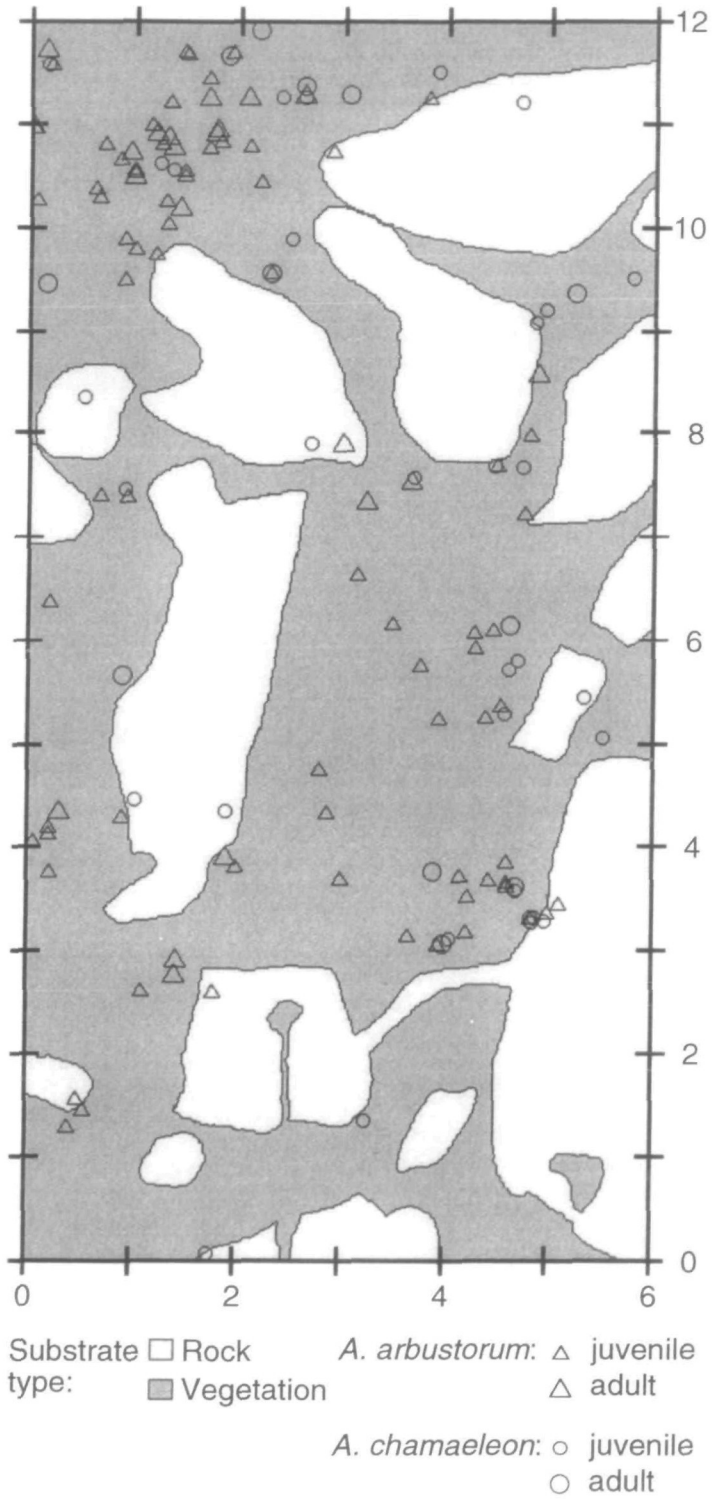


Figure 1b.

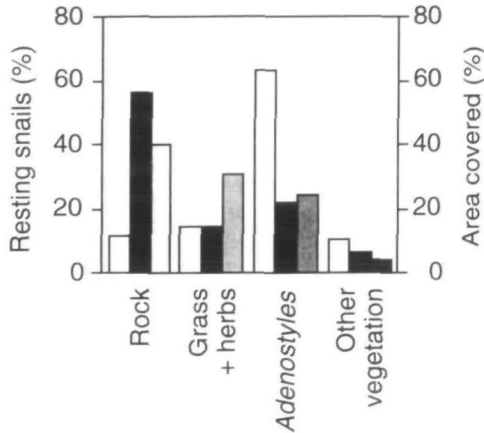


Figure 2. Percentage of resting snails (\square *A. arbustorum* and \blacksquare *A. chamaeleon*) attached to different substrates, and percentage of area covered by \blacksquare rocks, patches of \blacksquare grass and herbs, \blacksquare *Adenostyles*, and \blacksquare other vegetation. Other vegetation includes *G. sanguineum*, *C. spirasissimum*, *Salix* sp., *V. album*, *A. napellus* and *Peucedanum* sp.

more frequently attached to rock surfaces (juveniles: $\chi^2 = 62.88$, d.f. = 4, $P < 0.001$; adults: $\chi^2 = 61.26$, d.f. = 3, $P < 0.001$). Thus, the two species differed significantly in their resting-site preference.

Comparing the age classes within species, juvenile and adult *A. chamaeleon* did not differ in resting-site preference (Table 1; $\chi^2 = 0.25$, d.f. = 3, $P > 0.3$). In contrast, juvenile and adult *A. arbustorum* slightly differed in resting-site preference (Table 1; $\chi^2 = 14.33$, d.f. = 5, $P < 0.02$). This age-specific difference was mainly due to the smaller proportion of juvenile *A. arbustorum* which rested attached to rock surfaces and to the higher proportion of juveniles found in patches of *Adenostyles* (Table 1).

Arianta arbustorum was mainly found at the base of the NNE-exposed slope (in the first 12 m of the 38-m long belt), whereas *A. chamaeleon* occurred in all parts of the slope (Fig. 3). The difference in the spatial distribution between the two snail species can be explained by the distribution of rocks and patches of different vegetation in the investigation area (Fig. 3). The density of *A. arbustorum* was positively correlated with the percentage cover of *Adenostyles alliariae* (data from 2-m strips combined: $r = 0.85$, $N = 19$, $P < 0.001$) and negatively correlated with the percentage cover of rocks ($r = -0.59$, $N = 19$, $P = 0.007$). In contrast, the density of *A.*

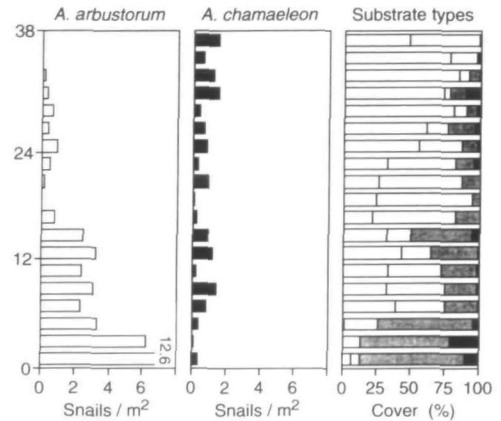


Figure 3. Density of *A. arbustorum* and *A. chamaeleon* over a 38-m gradient on the NNE-exposed slope (plot A) compared with the percentage cover of rocks and different types of vegetation (\square rocks, \blacksquare grass and herbs, \blacksquare *Adenostyles*, and \blacksquare other vegetation). Data on snail density and cover of rocks and different plants were combined for strips of 2×5 m.

chamaeleon was positively correlated with the percentage cover of rocks ($r = 0.47$, $N = 19$, $P = 0.04$). The densities of the snail species were uncorrelated ($r = -0.24$, $N = 19$, $P = 0.33$).

Resting-site preferences on the SSW-exposed slope (plot B)

Plot B did not contain distinct patches of different vegetation and was too small to allow a detailed data analysis. However, as in plot A, individuals of *A. chamaeleon* rested more frequently attached to rock surfaces (20.5%) than individuals of *A. arbustorum* (8.4%; $\chi^2 = 4.06$, d.f. = 1, $P < 0.05$). Comparing both plots (slopes), a smaller proportion of *A. chamaeleon* rested attached to rock surfaces in plot B than in plot A (20.5% vs. 56.6%; $\chi^2 = 17.43$, d.f. = 5, $P < 0.001$). In contrast, the two plots did not differ in the percentage of *A. arbustorum* resting attached to rock surfaces (plot A: 11.9%; plot B: 8.4%; $\chi^2 = 0.95$, d.f. = 1, $P > 0.3$).

DISCUSSION

The present study shows that individuals of both species were aggregated on both slopes. Similar patterns of spatial distribution were recorded in populations of *A. arbustorum* that

lived in uncultivated meadows, alpine pastures and a field of scree material with a few small vegetation patches (Andreassen, 1981; Baur, 1984, 1986). An aggregated pattern of snail distribution could reflect the small-scale heterogeneity of the environment (patches with different suitability; e.g. soil moisture), and/or it could result from the snails' behaviour to minimize the risk of predation, or in adults to find mating partners. Moreover, juveniles could be found aggregated due to their limited dispersal ability. Experiments are needed to distinguish between these hypotheses. However, the following observations contradict the assumption of limited dispersal in juveniles. Newly-hatched *A. arbustorum* moved on average 13.8 cm from the place they emerged in the first three days of life (Baur, 1988). The juveniles considered in the present study had much more time to disperse, because they measured 5 mm or more in shell breadth and thus were at least 1 year old (Baur & Raboud, 1988). It therefore seems unlikely that the aggregated distribution pattern of juveniles was due to their limited dispersal ability.

Baur (1984, 1986) found that in alpine populations *A. arbustorum* preferentially rested in aggregations. The size of the aggregations was partly related to the size of the shelters, while the number of snails found in an aggregation seemed to be influenced by weather, season and the animals' behaviour during the mating period (Baur, 1984, 1986). Similarly, Andreassen (1981) observed that juvenile and subadult *A. arbustorum* were always aggregated in a population near Bergen (Norway), whereas adults were only aggregated in their main mating period (May and June). The present study suggests that the aggregated distribution pattern of resting snails might partly be a result of substrate preference. Most probably the aggregated distribution of *Arianta* cannot be explained by a single factor.

Patterns of spatial distribution may be influenced by the proportion of snails found. During the activity season, *A. arbustorum* frequently rests for periods of up to several days buried in the soil (Baur & Baur, 1993). In many species a proportion of snails remain inactive in the soil even under conditions favourable for activity (Peake, 1978). We might have overlooked individuals buried in the soil and hidden in small fissures or in dense vegetation. This might be particularly true for juveniles. However, we do not assume that snails bury at places where absolutely no individuals were recorded (in that case snails

would have to move large distances between periods of activity and resting).¹ However, it is also possible that *A. arbustorum* and *A. chamaeleon* differed in the proportion of hidden individuals. Mark-release-recapture techniques have to be used to obtain accurate estimates of population size.

The present study shows that a difference in resting-site preference is one of the factors that distinguish the species ecologically. In plot A, *A. arbustorum* showed a preference for resting attached to leaves of *Adenostyles*, whereas *A. chamaeleon* preferred to rest on rock surfaces. Both species tended to avoid patches dominated by grass. In food-choice tests, *A. arbustorum* rarely consumed grass (Frömming, 1954). Preliminary observations indicate that *A. chamaeleon* feeds more frequently on algae and lichens than *A. arbustorum* (Dolt, Baur & Baur, in prep.). Differences in resting-site preference could be due to different utilization of food resources. In northern Greece, five coexisting species of land snails could be differentiated by the plants to which they were attached (Hatzioannou, Eleutheriadis & Lazaridou-Dimitriadou, 1994). In summer and autumn the snails consumed plant material in proportion to the occurrence of these plants, although one of the most abundant plant species (*Hedera helix*) was not eaten at all. Grime & Blythe (1969) studied the relationships between the occurrence of *A. arbustorum* and plant species at the Winnats Pass in Derbyshire, England, and found that *A. arbustorum* was positively associated with *Mercurialis perennis* and *Urtica dioica* and negatively associated with grass (mainly *Festuca rubra*). Grime & Blythe (1969) examined resting sites and faeces of *A. arbustorum* and concluded that the snails fed mainly upon the plant materials to which they were attached during the day. However, this must not always be the case.

Differences in resting-site preference could also be explained by different adaptations against predation and/or insolation. The paler shells of *A. chamaeleon* might be more cryptic on limestone rock surfaces and absorb less thermal radiation than the darker shells of *A. arbustorum*, which in turn may be better protected against predators when they are attached to the underside of leaves of *Adenostyles* (cf. Abdel-Rehim, 1983; Burla & Gosteli, 1993). Patches of dense vegetation retain more humidity than their surroundings and mitigate extreme temperature fluctuations. It is possible that *A. arbustorum* exhibits a lower resistance

to desiccation than *A. chamaeleon*. However, experiments are needed to understand the adaptive significance of resting-site preferences in these snail species.

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