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Animal Biology 62 (2012) 451–462

Animal Biology
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Differences in population dynamics of *Bradybaena fruticum* (O.F. Müller, 1774) (Gastropoda: Pulmonata: Bradybaenidae) in a submontane and lowland area of Poland

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Accepted: April 22, 2011

Abstract

Population dynamics of a meso-hygrophilous helicoid *Bradybaena fruticum* was studied in SW Poland at two localities with similar habitat but different climatic conditions. Unexpectedly, at the submontane site in Szczytna the growth appeared to be significantly faster than in the lowland site (Wrocław), where the weather conditions varied widely during the whole growing season. In Szczytna the average growth rate was 0.26 whorl/month; 0.36 whorl/month in the fast phase (juveniles from hatching till 5.0 whorls), and 0.07 whorl/month in the slow phase (snails with 5.1 whorls till lip formation). During the whole growing season, the average increment was 4.5 whorls, whereas the maximum was 5.45 whorls. In Wrocław the average growth rate was 0.05 whorl/month; 0.1 whorl/month in the fast phase, and only 0.01 whorl/month in the slow phase. The average growth of juveniles, estimated during two growing seasons, equalled 3.8 whorls; the maximum recorded value was 4.75 whorls. In the winter there was hardly any growth. In earlier studies it was found that at higher altitude the growth rate seems to decrease and therefore appears to be correlated with the thermal regime of the locality. In this study it was established that the weather patterns, like months with drought or occasional flooding, are likely to influence the population dynamics in the lowland population.

Keywords

Size structure; growth rate; humidity; flooding; land snail; *Bradybaena fruticum*

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DOI 10.1163/157075612X650131

Introduction

Life-history traits in terrestrial gastropods may be influenced by both abiotic and biotic factors. Intra- and inter-population variation in reproductive patterns in response to various proximate factors such as climatic pressures or population density has been documented, among others, in *Cepaea nemoralis* (Wolda and Kreulen, 1973; Oosterhoff, 1977), *Theba pisana* (Cowie, 1984), *Arianta arbustorum* (Baur and Raboud, 1988) and more recently in *Xeropicta derbentina* (Kiss et al., 2005), *Xerolenta obvia* (Lazaridou and Chatziioannou, 2005) and *Vestia gulo* (Sulikowska-Drozd, 2011).

The present study focuses on a variation in the life cycle and population dynamics of *Bradybaena fruticum* (O.F. Müller, 1774) recorded in two populations in SW Poland. *B. fruticum* is a medium-sized, hermaphroditic, pulmonate snail and the only member of the family Badybaenidae found in Europe. The distribution range of the species covers nearly entire Europe from the Urals and Caucasus to the Balkan Peninsula, the southern part of Scandinavia, Germany, the western part of France and northern Italy (Shileyko, 1978; Kerney et al., 1983; Riedel, 1988). It inhabits scrub and sparse woodlands, often close to the water bodies, sometimes also grassland, parks and gardens, preferring herb and nettle patches, and it is mesohygrophilous (Bába, 1985). In Poland, this is one of the most widely distributed land snail species, practically found all over the country, and in the mountains reaching altitudes of 900 m a.s.l. (Wiktor, 2004).

Only a few studies have dealt with the biology and life cycle of *B. fruticum* (Künkel, 1928; Bába, 1985; Staikou et al., 1990; Seifert and Khokhutkin, 2009). In northern Greece, the snail reaches maturity at the age of 21 months when the largest shell diameter exceeds 19.3 mm (Staikou et al., 1990), whereas in central Europe the maturity is reached within 13-14 months (Frömming, 1954; Bába, 1985) at the shell height of 12-14 mm. The life span is 5-6 years, but some specimens may survive 10 years (Staikou et al., 1990). The mean clutch size of eggs laid in Greece is 44.2 $\pm$ 8.6; hatching takes place 20-25 days after egg-laying (Staikou et al., 1990). The reproductive period starts at the beginning of summer; the snails grow during the spring and autumn and the main part of the population consists of two cohorts; the third cohort of juveniles is added after the spring-summer reproductive period (Staikou et al., 1990). Under laboratory conditions the time to reach maturity depends on the period of hatching and varies from 15-16 to 21-22 months at the shell width of 17 mm and height of 12 mm (Künkel, 1928). Reproduction can take place several times in the season, starting from the second year of life; 3-76 eggs per clutch are laid and their total number per laying period per individual varies from 180 to 255 in the third laying period, but decreases to 44-60 in the fourth laying period (Künkel, 1928).

This paper reports on a life cycle and population dynamics of *B. fruticum* at two sites, situated over 100 km apart, with similar habitats and exposed to different climatic conditions.

Material and methods

The study was carried out from May till November 2009 and 2010 in Wrocław and from May till September 2010 in Szczytna (in October 2010 the population was affected by clear-felling and heavy vehicles disturbance). The main habitat characteristics of the sampling sites are given in table 1. Figures 1A-B show temperature and precipitation regimes at each site during the study period.

Seasonal changes in the size structure were traced based on regular samples (visual search) being taken monthly. On each occasion snails were collected during 2 hours, from an area of 20 m^2. Growth rate and longevity estimate in the field were based on monthly marking with nail varnish (each month a different colour). Marking consisted in painting a narrow stripe on the shell, just next to the aperture margin, so that the shell increment could be read on recapture. For each recaptured individual the whorl increment since the last marking and the date of the last marking were noted, then the individual was marked and released. The average growth rate was estimated for all marked-recaptured snails in both populations. Because of large differences in the ultimate size (shells of the same size may have a different number of whorls) the growth rate was expressed by whorl increment, like in other studies (Pokryszko, 1990; Maltz, 2003; Kuźnik-Kowalska, 2005; Kuźnik-Kowalska and Roksela, 2009). Whorls were counted according to Ehrmann's (1933) method and seven size classes were distinguished (table 2).

The differences in shell growth between the populations were tested using Mann-Whitney U test which evaluates differences in medians. Statistica PL 6.0 and Microsoft Excel 2007 were used for statistical analysis of the data.

Table 1.
Habitat characteristics of sampling localities.

Locality (geographical area)	Wrocław (Silesian Plain)	Szczytna (Central Sudetes)
Coordinates	N 51°08′59.81″ E 16°57′25.91″	N 50°24′07.86″ E 16°27′49.72″
Altitude a.s.l.	112 m	460 m
Habitat type	lowland	submontane zone
Plant community	mainly *Urtica dioica*, single willow (*Salix fragilis*) and hornbeam (*Carpinus betulus*) trees	mainly *Urtica dioica*, single alder (*Alnus glutinosa*) and beech (*Fagus sylvatica*) trees
Canopy	40%	40%
Herb layer	70%	60%
Length of growing season*	226 days	189 days

* Data from Dubicki et al., 2002; Stanisławska et al., 2004.

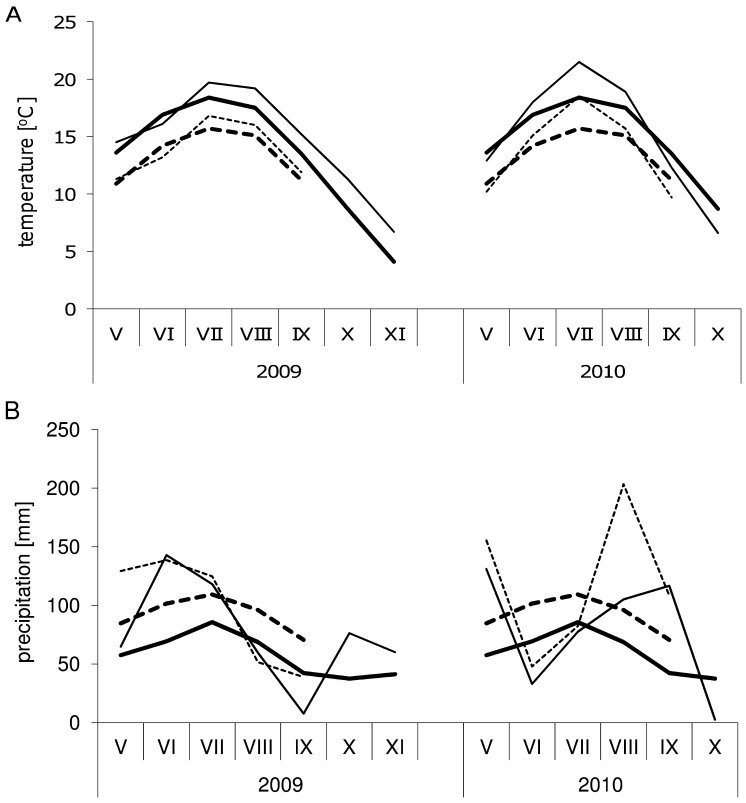

Figure 1. Mean monthly temperatures (A) and total monthly precipitation (B) during the study period vs. long-term means (bold lines) in Wrocław (fine solid line) and Szczytna (fine dotted line). Data from Biuletyn Meteorologiczny published on-line: www.meteo.uni.wroc.pl and from Słoszów meteorological post (IMGW data).

Results

In the field *B. fruticum* was found directly on herbs or climbing shrubs and trees to the height of three metres.

Table 2.
Size classes of *B. fruticum*.

Size class	Number of whorls
I	2.0-3.0
II	3.1-3.5
III	3.6-4.0
IV	4.1-4.5
V	4.6-5.0
VI	5.1-5.4
VII	⩾5.5

Population size structure

Size structures of the two populations are shown in figs. 2A-B. The youngest snails (2.0-3.0 whorls; table 2) appeared first in May in the Wrocław population, while in Szczytna they were present from May to September at a similar quantity. The number of individuals from the second size class (3.1-3.5 whorls) started to increase in abundance in August throughout September and reached its peak in October (Wrocław 2009); in Szczytna they occurred throughout all months at a similar quantity. Snails of size class III (3.6-4.0 whorls) appeared in all months at both sites, having the peak abundance in September (Wrocław) and July (Szczytna). Size class IV (4.1-4.5 whorls) was also present in all months with peaks in September and October (Wrocław), and in August (Szczytna). The abundance of subadults from size class V (4.6-5.0 whorls) fluctuated during a period of the whole growing season at both sites and started to decrease drastically in November (Wrocław) and September (Szczytna). The largest number of adults (size classes VI and VII) was noticed

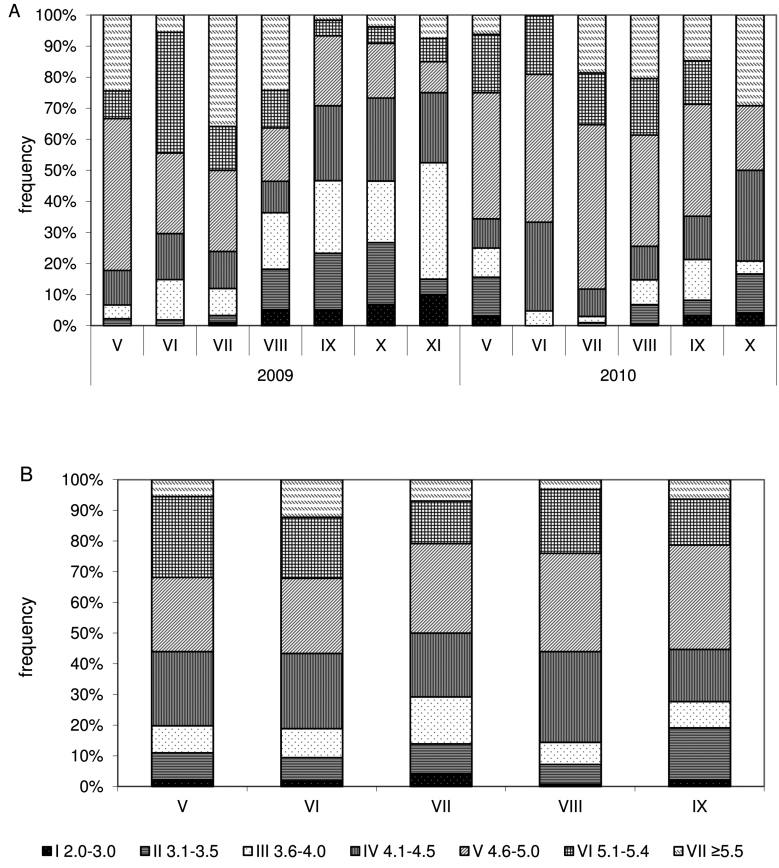

Figure 2. Changes in the percentages of size classes over the activity seasons 2009 and 2010 in Wrocław (A) and 2010 in Szczytna (B).

in July and August (Wrocław), and in May and June (Szczytna). The proportion of juveniles (size classes I-V) in the Wrocław population was the smallest in July 2009 (50%), and then started to increase gradually from August (63%) reaching ca. 90% in September and October. In the Szczytna population the proportions in consecutive months varied from 68% to 78%. In general, the surveyed populations were dominated by juveniles.

Growth

The standard statistics (mean, variance, standard deviation and median) of whorl increment in the consecutive size classes at the two studied sites are shown in table 3.

The total number of individuals collected on each occasion in Wrocław ranged from 45 to 131 (2009) and from 21 to 176 (2010). Among the 1058 marked snails, 154 (14.5%) were recaptured once, 18 (1.7%) were recaptured twice and 4 (0.38%) were recaptured three times.

During the lifetime of snails the differentiated growth rate might be distinguished: the fast phase recorded for snails with 2.0-5.0 whorls and the slow phase for those with 5.1 and more whorls (till lip formation) (table 3). The average growth rate, based on recaptures and growth readings, was 0.05 whorl/month. In the fast phase it was 0.1 whorl/month and only 0.01 whorl/month in the slow phase. Taking into account the fact that *B. fruticum* when hatching has 2.0 whorls (Künkel, 1928), snails reached approximately 3.8 whorls within 210 days, while the maximum recorded value was 4.75 whorls (fig. 3). In winter and early spring, the maximum whorl increment was very limited and the snails managed to grow up by 0.35 whorl per six-month period (from late October until early May).

In the Szczytna population the number of individuals collected on each occasion ranged from 47 to 125, and the total number of marked snails was 442: 69 (15.6%) were recaptured once and 7 (1.6%) were recaptured twice. The average growth rate was 0.26 whorl/month; 0.36 whorl/month in the fast phase, and 0.07 whorl/month in the slow phase. The average whorl increment, estimated for the recaptured juveniles

Table 3.
Whorl increment per month in *B. fruticum* at two studied sites. Comparison of size classes expressed by number of whorls.

No of whorls	Wrocław					Szczytna					Mann-Whitney U test
	Mean	Min-max	*SD*	Median	*N*	Mean	Min-max	*SD*	Median	*N*	
3.0-3.5	0.14	0-0.40	0.15	0.10	6	0.50	0.25-0.75	0.17	0.50	6	$P = 0.018$
3.6-4.0	0.11	0-0.45	0.12	0.08	24	0.45	0.10-0.75	0.19	0.50	8	$P < 0.001$
4.1-4.5	0.06	0-0.25	0.07	0.05	18	0.29	0.10-0.55	0.13	0.30	28	$P < 0.001$
4.6-5.0	0.05	0-0.15	0.05	0.05	66	0.22	0.00-0.35	0.10	0.22	23	$P < 0.001$
$\geqslant$5.1	0.01	0-0.10	0.02	0.00	52	0.07	0.00-0.25	0.08	0.05	17	$P = 0.002$

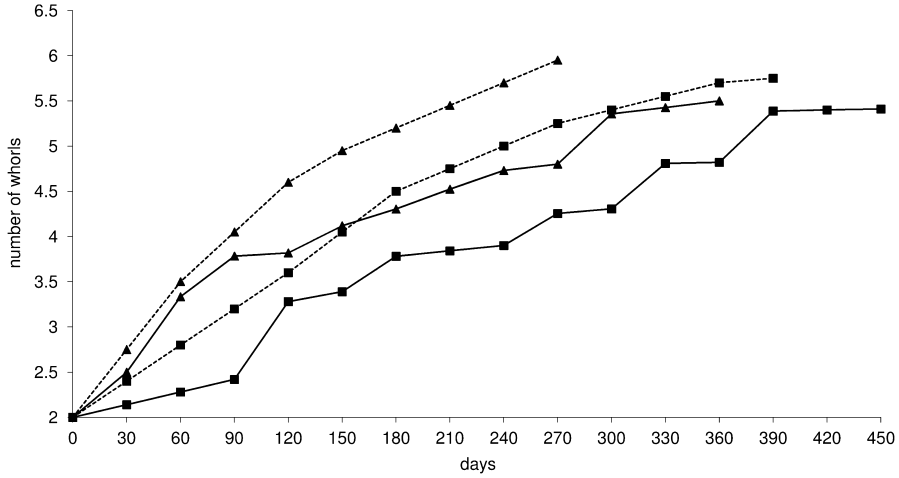

Figure 3. Growth rate of *B. fruticum* at the studied sites. Triangles – Szczytna, squares – Wrocław, solid line – mean whorl increment, dotted line – maximum whorl increment.

within the period of 210 days was 4.5 whorls, whereas the maximum recorded value was 5.45 whorls (including 2.0 whorls when hatching) (fig. 3).

The shell growth rate between the studied populations was compared using a Mann-Whitney U test. The results showed that it was significantly slower in Wrocław than in Szczytna (table 3).

Out of 442 specimens, sampled from Szczytna, 37 (8.4%) appeared to be snails with reflected lip which indicates growth termination and maturity. The number of whorls of such snails ranged from 5.1 to 6.0 (mean 5.6, $SD = 0.21$). In Wrocław, the total number of mature snails was 140 (13.2%) and their number of whorls ranged from 5.0 to 5.75 (mean 5.34, $SD = 0.1$).

Discussion

Population size structure

Seasonal changes in the size structure of the studied populations, combined with the growth rate, make it possible to reconstruct the life cycle of *B. fruticum*. The smallest snails, representing the two youngest classes that occurred from May till November, suggest that in the wild *B. fruticum* laid eggs throughout the vegetation season. The earliest hatched snails grew to ca. 4 whorls in their first season; most juveniles wintered over when their shells had 2.6-3.5 whorls. The mean time required to form one whorl in juveniles (first growth stage) was 90-120 days (ca. 0.3 whorls per month). Adult size was reached in the following season. Snails of the oldest size class were present during the whole season, but were the most numerous in July and August.

The size structure pattern of *B. fruticum* was not rigid and variations occurred from one year to the next and were different at both localities. It is noteworthy that

the juvenile/adult proportion in Szczytna was identified as being more stable during the whole growing season when compared with Wrocław where, during 2009 and 2010, the proportion changes were fluctuating widely. It is likely that a combination of environmental characteristics such as weather and/or climatic conditions is an important factor in controlling growth and size structure of the species (see also Discussion: Growth).

Growth

Data on the growth rate from field observations indicate that the growth is the quickest among the youngest snails and its rate gradually decreases in consecutive size classes at both studied locations (table 3). The differences between the two populations are significant and may be explained, besides by internal factors, mainly by environmental conditions such as variable temperature and/or humidity associated with the site, and aestivation during the hot and dry periods. These factors had an essential influence on the growth of snails in Wrocław. It was clearly noticeable that the growth was considerably decelerated in August and September 2009 when precipitation was extremely low (fig. 1B). After the 3rd of August when a significant rainfall took place (daily sum: 37.4 mm, 63% of total monthly rainfall), the remaining days of August and the whole September could be classified as extremely dry (figs. 4A-B; Ropuszyński, 2009; Sawiński, 2009). The sum of precipitation in September was remarkably low and equalled only 7.7 mm, which constituted merely 16.1% of the monthly norm. Moreover, both months were very warm, with daily mean temperatures of 19.2°C (August) and 15.2°C (September), which exceeded average long-term values by 1.5°C and 1.9°C, respectively (Ropuszyński, 2009; Sawiński, 2009; fig. 1A). The weather was also characterized by relatively high values of daily sunshine duration in these months (Ropuszyński, 2009; Sawiński, 2009). Thus, the captured snails were found aestivated on tree branches and shrubs or hidden inside curled dry leaves. On the other hand, in May 2010 extremely abundant rainfall in Wrocław was recorded (only 6 rainless days) with the monthly sum of 131.0 mm (fig. 4C). It was more than twice as high as the mean long-term value (53.9 mm) (Korzystka, 2010; fig. 1B). This resulted in a flooding and a significant population loss of *B. fruticum* in the studied area. The phenomenon had a catastrophic effect mainly on the newly hatched and young snails with less than 4.0 whorls (fig. 2A).

Not only climatic factors such as temperature and precipitation regimes differ between the two studied sites, but also the length of the growing season, which in Wrocław is by 37 days longer than in Szczytna (table 1) and belongs to the longest in Poland (Dubicki et al., 2002). The latter factor is, among others, associated with the altitude that differs by ca. 350 m. The differences in growth rate observed between the studied populations were substantial. In the Wrocław population the growth of snails actually stopped during the two-month drought in 2009. In Szczytna, however, *B. fruticum* remained active practically during the whole growing season which resulted in a continuous growth, presumably due to the sufficient

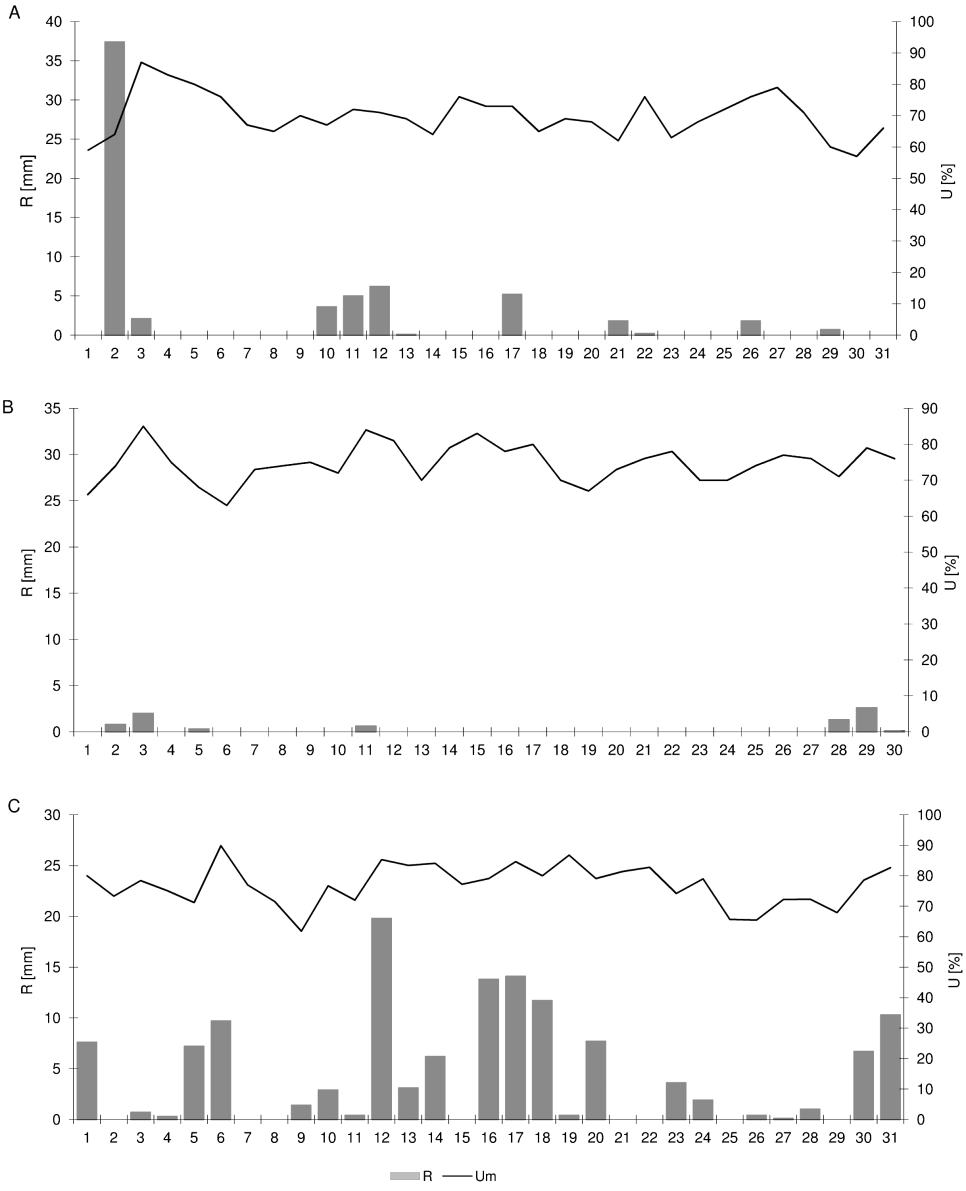

Figure 4. Relative humidity (U) and daily precipitation sums (R) in Wrocław in: August 2009 (A), September 2009 (B), May 2010 (C). Um – daily mean humidity. Data from Ropuszyński (2009), Sawiński (2009), Korzystka (2010).

humidity. Lower or at least a similar level of precipitation in Wrocław is evidenced by both mean monthly data, recorded during the activity season (May-October), and long-term means (fig. 1B). Additionally, it is noted that Wrocław is the city with low precipitation which constitutes ca. 50% of the total precipitation in high-

lands (Dubicki et al., 2002). In this regard, our results are not in accordance with the data obtained in the earlier studies for *Vitrina pellucida* and *Semilimax kotulae* (Umiński, 1975), and *Vestia gulo* (Sulikowska-Drozd, 2011) in the Polish Carpathians. In these studies the growth rate was found to decrease with increasing altitude which was correlated with the thermal regime of the locality. In *Arianta arbustorum* the prolonged time to reach maturity has been reported not only at high altitudes (Baur, 1984), but also in populations inhabiting the northern edge of its distribution, namely southern Finland (Terhivuo, 1978).

However, in the Mediterranean region the factor humidity, rather than temperature, influences the variation of life history variation. According to Lazaridou and Chatziioannou (2005), the growth of *Xerolenta obvia* in northern Greece was dependent on rainfall. In that type of climate, aestivation and thus cessation of growth during hot summer, seems to be the safest strategy to survive untill the autumn rains. Similar observations were made on *B. fruticum* from Greece, in which decreased growth rate was observed in autumn. This was explained by a possible correlation with the dry weather conditions during that time (Staikou et al., 1990). In *Xeropicta arenosa*, depending on the habitats of differing humidity regimes, seasonal variations in growth rate were recorded or not. The lack of seasonal variation in growth could be considered as resulting from a behavioural response of this xerotheromphilic species to an environment characterized by long, wet periods in midsummer (Staikou and Lazaridou-Dimitriadou, 1991).

Despite the smaller precipitation in Wrocław, it is clear that both populations retain an essentially temperate breeding season: mating, egg-laying and hatching occur in the late spring and early summer. In this respect, both populations differ from those of helicoid species in the Mediterranean climate further south, where summer is not a suitable time for egg laying, hatching and growth (Lazaridou and Chatziioannou, 2005). However, some weather anomalies, like drought or occasional flooding occurring in *B. fruticum* habitat, may considerably affect its population dynamics and influence the duration and timing of the breeding season.

Acknowledgements

This paper was written thanks to invaluable help and involvement of Prof. Beata M. Pokryszko. We are also indebted to two anonymous reviewers for their helpful comments and constructive suggestions which have improved the manuscript considerably.

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