Cent. Eur. J. Biol. • 8(7) • 2013 • 693-700
DOI: 10.2478/s11535-013-0182-5

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Central European Journal of **Biology**

Reproduction, growth and circadian activity of the snail *Bradybaena fruticum* (O. F. Müller, 1774) (Gastropoda: Pulmonata: Bradybaenidae) in the laboratory

Research Article

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Received 29 August 2012; Accepted 11 March 2013

Abstract: Selected life cycle parameters of the snail *Bradybaena fruticum* were studied in the laboratory. The initial material for the laboratory culture was taken from a population in South Western Poland; the snails were kept in Petri dishes and plastic containers. The temperature, humidity and lighting conditions were maintained at a constant level (day 18ºC, night 12ºC, rh 80%, light:dark 12:12). Circadian activity observations were conducted outside the climatic chamber. Eggs – calcified, slightly oval, of mean dimensions 2.67x2.56 mm – were laid singly or in batches of 6-62, as a result of both biparental and uniparental reproduction. Incubation took 27-76 days and hatching was asynchronous. Hatching success was lower among eggs produced by single parents compared to eggs produced by two parents (*c.a.* 56 and *c.a.* 88%, respectively). Growth included fast (2.25 to 5 whorls) and slow (1.9-2.25 and >5 whorls) phases as well as lip formation, and took 261 to 420 days. The first eggs/batches were laid *c.a.* one year later, and for uniparentally reproducing snails the period was even longer. The growth of snails kept singly was faster than in those kept in groups. Juvenile snails were much more active than adults in the spring, summer and autumn but the adults were more mobile in the winter. In all seasons, juveniles were more active at night than adults.

Keywords: *Life history • Uniparental reproduction • Land snail • Bradybaena fruticum • Bradybaenidae*

1. Introduction

The snail *Bradybaena fruticum* (O. F. Müller, 1774) (Gastropoda: Pulmonata: Bradybaenidae) is the only European bradybaenid. It is an East-European species, reaching the Urals and the Caucasus in the East, France in the West, the Balkans in the South and southern Scandinavia (65˚N) in the North [1]. B. *fruticum* is found throughout Poland except in mountains, at high altitude (Karkonosze, higher parts of the Tatra, Babia Góra, high altitudes in the Bieszczady). It is very common in the lowlands, less so in the mountains and highlands, and only local in the Beskidy Mts and the Sudetes [2]. *B. fruticum* is euryoecious. It occurs in damp places with lush herbs in forests, scrub, on river banks, in parks and in wet meadows where it feeds on decaying and fresh plant material (*i.e. Urtica dioica* L., *Aegopodium podagraria* L.). It is usually found crawling on plants or attached to the underside of big leaves and it spends dry periods in leaf-litter.

Information on the life cycle, reproduction and population dynamics of this species is important for evolutionary and phylogenetic inferences, community ecology and conservation. However, as with many European terrestrial gastropods, very little is known about this species. The life cycle of *B. fruticum* has been studied only partially [3-5] since this species has been of interest mainly to population geneticists [6-12]. The objective of our study was to describe selected aspects of the life cycle of *B. fruticum* based on laboratory observations. For field observations on the species, see Proćków *et al.* [13].

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2. Experimental Procedures

The initial material for the laboratory culture of *B. fruticum* (6 adults) was collected on the 30th of June 2009 near the Milennium Bridge in Wrocław (SW. Poland, 51º07'52.03"N; 16º59'24.70"E). From June 30th 2009 until February 8th 2011, the snails produced 47 egg batches; 76 of the individuals that hatched constituted the original laboratory population.

The snails were kept in Petri dishes and in containers with different sizes depending on the number of individuals (dishes of 6-10 cm diameter, glass vivarium of 20×15×18.5 cm, plastic containers of 15.5×12.5×5 cm, 6×7.5×5 cm and 12×7.5×5 cm). The substratum consisted of a layer of damp tissue paper with a thin layer of gardening soil (natural, with no supplements) on top. All the eggs found were transferred to dishes lined with tissue paper, and they were covered with tissue paper. The dishes and containers with snails were kept in a climatic chamber at constant conditions of temperature (day 18ºC, night 12ºC) and humidity (80%), with a 12:12 h light regime (fluorescent lighting). Holes in the lid of the containers ensured proper aeration and the substratum was changed at least once a week. Water and food were supplied as needed. The snails were fed lettuce, cabbage, carrot, apple and cucumber. Dolomite tablets constituted the source of calcium.

The observations were to ascertain the capability/incapability of uniparental reproduction, egg laying, fecundity, incubation, hatching, possible cannibalism, growth, maturation, life span, and seasonal activity. Fragmentary field observations of mating were also used.

Growth rate was assessed through counting whorls every 30 days using Ehrmann's method [14]. To check the possibility of uniparental reproduction, 23 snails were kept singly in plastic containers of 12×7.5×5 cm or dishes of 6-10 cm diameter from early juvenile stages until death. The remaining snails were kept in groups of 2-10 individuals: 1 group of 2 individuals, 1 group of 3 individuals, 1 group of 8 individuals and 4 groups of 10 individuals. The maximum reproduction was estimated by summing the number of eggs produced each month for consecutive months by 10 snails, starting on February 5th 2010. To ascertain fecundity and hatching success, the egg-laying places were searched, the eggs and hatchlings counted, and the incubation time recorded. The time of egg-laying was recorded once, for 10 eggs in a single batch, since the process of egg-laying was observed directly only once. The eggs (n=30) were measured with a calibrated eyepiece to the nearest 0.025 mm. To test cannibalism, hatchlings (test 1) and adults (test 2) were offered conspecific and non-conspecific (*Succinea putris*) eggs. Circadian activity was assessed based on 24 hour observations (the behaviour being checked every hour) of 10 juveniles and 10 adults during spring, summer, autumn and winter. The observations were conducted in the laboratory, outside the climatic chamber, using necessary lighting (dim lamp in the corner of the room), within the temperature range of 18-23ºC. A five-grade scale of activity was used: full activity, *i.e.* crawling, feeding, mating, egg-laying (100%); foot extended, tentacles moving (75%); extended foot and tentacles everted but not moving (50%); foot extended, tentacles retracted (25%); completely retracted, no activity (0%). Life span was assessed as the number of days from hatching to the time of death; the number of days from hatching until lip formation (morphological maturity) was also counted. Statistical analysis was done with Microsoft Excel 2007.

The reproduction of the laboratory population and the growth of selected individuals were observed from February 5th 2010 until April 6th 2011.

3. Results and Discussion

3.1 Egg laying, incubation and hatching

No mating was observed in the laboratory; the last phase of copulation was observed once in the field. Each of the two partners was then placed in a separate container. The time between copulation and egg-laying was 53 days. The copulation took place on 4.05.2010, and on 26.06.2010 the first snail laid 22 eggs in a single batch. The second snail laid eggs (2 singly and 13 in a batch) 69 days after copulation (12.07.2010).

B. fruticum laid eggs under damp tissue paper, on the bottom of the container, in the soil and under lettuce leaves. Laying of one egg lasted 11 to 30 minutes (mean=20.4; SD=6.0; n=10). Having produced a batch, the snail moved away without covering the eggs with mucus. Eggs were laid from February until September (5.02.2010 – first batch; 20.09.2010 – last batch) by snails kept in pairs or groups. The number of eggs produced during that period was 1057, in 48 batches, and 20 as single eggs. The most numerous eggs were laid in February and July. Uniparental reproduction was observed on three occasions: 7.07.2010 (19 eggs), 28.02.2011 (8 eggs) and 17.03.2011 (17 eggs) (Figure 1). The eggs were slightly oval, nearly spherical, milky white, calcified, slightly shiny. As the eggs approached hatching, the egg envelope became increasingly darker, thinner, softer and more translucent. Eggs that did not hatch gradually turned opaque, more brown and then decomposed. The uni- and biparentally produced eggs differed only in size. The comparison of some life cycle parameters between uni- and biparentally reproducing snails of *B. fruticum* is shown in Table 1.

Incubation time varied widely and hatching was asynchronous (Table 1). The first sign of hatching was a fragment of egg shell breaking off. The hatching success among eggs produced by parents kept in pairs or groups was 88.36% (638 juveniles hatched from 722 eggs); the hatching success among uniparental eggs was 56.41% (22 hatchlings from 39 eggs). This difference was statistically significant (χ^2=11.55; P=0.05; df=1). The shells of biparental hatchlings had 1.9-2.25 whorls (mean=2.06; SD=0.09; n=66). They were translucent, light brown, with no hairs; the dark-spotted mantle could be seen through the shell. The hatchlings were very active; they first ate their own egg envelopes and then wandered away in search of other food. No egg cannibalism was observed among juveniles or adults, even in the absence of other food; likewise, no adult-juvenile cannibalism occurred. Non-conspecific (*Succinea putris*) eggs were not consumed by either juveniles or adults.

The only other bradybaenid whose life cycle has been studied is the Asian *B. similaris* [15,16]. In this species, the total number of eggs per batch varies from 1 to 38, and the total number of batches per snail is 1 to 6 [15]. In a study by Carvalho *et al.* [16], each group of 30 snails produced on average 22 egg batches and a total of 2700 eggs over the lifespan of the colony. The number of eggs per batch ranged from 1 to 202. Thus, the mean daily reproductive output during the adult stage varied between 0 and 398 eggs, or 0-79.5 eggs per individual. The number of eggs per batch as well as the number of egg batches in *B. fruticum* were fairly similar to that reported by Almeida and Bessa [15].

The mode of egg-laying observed in the laboratory confirms the observations of Künkel [17]. Apart from selecting damp and sheltered egg-laying places, no signs of parental care were observed. Eggs of

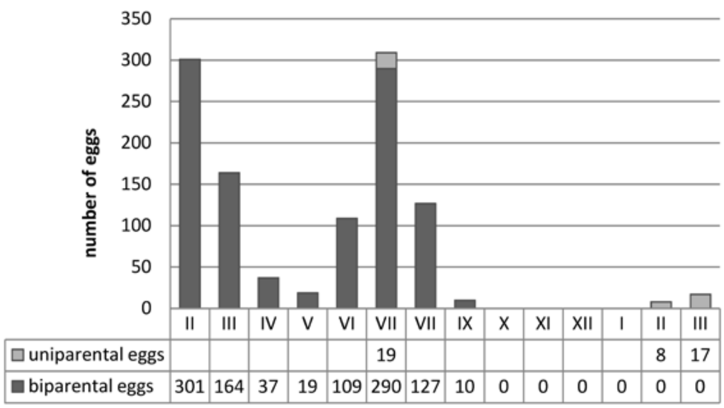

Figure 1. Reproduction dynamics of. *B. fruticum* in the laboratory: number of eggs recorded during consecutive months of observation.

Life cycle parameter	Uniparental				Biparental			
	Range	Mean	SD	n	Range	Mean	SD	n
Egg measurements (in mm)	2.59-3.17 x 2.37-2.80	2.74 x 2.59	0.13 x 0.10	30	2.34-3.17 x 2.18-2.95	2.67 x 2.56	0.13 x 0.13	120
Number of eggs per batch	8-19	14.70	5.86	3	6-62	23.60	13.47	49
Incubation time (days)	37-53	45.31	4.20	22	27-76	43.99	7.56	663
Days of hatching in the same batch	2-26	4.91	7.08	11	1-29	4.15	5.17	97
Days from hatching to egg laying	393-588	466	106.33	3	362-362	362	0.00	7*
Days from lip completion to egg laying	90-401	194.66	178.69	3	10-102	75.57	32.97	7*

Table 1. Comparison of uni- and biparental reproduction in *B. fruticum*.

**seven individuals were observed during their first egg-laying*

B. fruticum are very sensitive to desiccation; they break when the humidity is too low [17]. In studies conducted in northern Greece [5] the mortality of *B. fruticum* eggs was 35%; the main reason was probably desiccation. The eggs of *B. fruticum* are nearly spherical, calcified, milky white, of 2.34-3.17 mm in major diameter, which agrees with the observations of Künkel [17]. Staikou *et al.* [5] reported a mean major diameter of 1.98 mm.

Since our experiment was conducted in a climatic chamber (constant temperature and lighting conditions) and the individuals observed were not brought directly from the field, it is likely that their seasonal reproductive pattern was disturbed. Nevertheless, the two reproductive peaks (February and July) yielded numbers of eggs that were almost twice higher than those produced during the remaining part of the year. The likely reason for this pattern is the cycle of gamete production (mainly oogenesis) in the gonad [18]. Contrary to many other helicoids [19-28], *B. fruticum* did not cover its eggs with protective mucus, which is thought to act against desiccation and microorganisms [23,29].

The incubation period in our study varied widely, from 27 to 76 days. It is unlikely that temperature differences are responsible for these differences since conditions in the laboratory were constant. It is more probable that the differences resulted from the different time of egg retention, which is often caused by unfavourable environmental conditions [23]. According to Staikou *et al.* [5] the incubation time of wild *B. fruticum* in northern Greece is 20-25 days; the minimum time reported by Seifert and Khokhutkin [30] is 13-14 days. Such large differences might have resulted from the different climatic conditions of the studies. The eggs of the Asian *Bradybena similaris* take 14-35 days to hatch in the laboratory, which is quite variable [15]. Other species in which the incubation time varies very widely are *Perforatella bidentata* (8-34 days) [28] and *Helicodonta obvoluta* (14-31 days) [27].

In our study, the hatching success of *B. fruticum* kept in pairs and groups was 88.36% and was thus close to the result obtained by Almeida and Bessa [15] for *B. similaris* – 81.22%. Hatching in *B. fruticum* is asynchronous, spanning 1-29 days within a single batch. One of the explanations proposed is the position of the egg in the batch (either peripheral or central), which may affect the rate of development [27]. Like hatchlings of *Arianta arbustorum* [31], the hatchlings of *B. fruticum* consume their egg envelopes, but no egg cannibalism was observed in our studies contrary to the former species.

B. fruticum was found to be capable of uniparental reproduction, albeit with less success than in the case of biparental reproduction. Only three (13%) out of the 23 snails kept singly reproduced. In *B. similaris*, uniparental reproduction was observed to occur in 18.4% of induividuals [15], but the authors provide no data on the hatching success, egg size, number of eggs and batches. Although *B. fruticum* is capable of uniparental reproduction, it is much more successful when reproducing biparentally. Only a small proportion of individuals were able to reproduce uniparentally and they produced smaller egg batches which took longer to hatch. Hatching success was also much smaller. Individuals produced by a single parent take much longer to start reproducing (*cf.* Table 1). A similar phenomenon was observed in *B. similaris* [15]. Uniparental reproduction is very rare in helicoids; it is known in *Helix aspersa* [32], *Arianta arbustorum* [33] and *Microxeromagna armillata* [34].

3.2 Growth and maturation

The growth of *B. fruticum* could be divided in two phases. During the fast phase (2.25 to 5.0 whorls), the formation of one whorl took 54-123 days (mean=79.54; SD=31.99; n=10). During the slow phase (1.9-2.25 whorls and above 5.0 whorls), the formation of one whorl took 155 to 462 days (mean=253.51; SD=147.02; n=10).

The growth rate of snails kept in groups of ten per container (dimensions 12×7.5×5 cm), was slower than that of snails hatched on the same day (25.03.2010) and kept in separate containers (6×7.5×5 cm) after reaching *c.a.* 3.4 whorls. None of the snails kept in a group formed a lip, while eight of the snails kept singly formed lips before 6.04.2011. After about three months, mortality rates in the groups increased: among the 50 snails, 20 survived until 6.04.2011. The average growth of ten randomly selected snails that were kept singly (n=10) and the average growth of a randomly selected group of 10 individuals is presented in Figure 2.

Morphological maturity (lip completion) was reached at 5.5-6.0 whorls (mean=5.55; SD=0.07; n=23), 261 to 420 days after hatching (mean=338.59; SD=26.87; n=23). The shell width at lip completion was 15.89-18.17 mm (mean=16.99; SD=0.66; n=11) and the lip height was 12.12-15.33 mm (mean=13.69; SD=0.99; n=11). Shell growth after lip completion was small (the maximum whorl increment was 0.2). Sexual maturity is sometimes estimated based on the time of first egg-laying [35]. For snails kept in groups, the first batch was laid *c.a.* 12 months (362 days) from hatching (362-362; mean=362 days; SD=0; n=7). For isolated snails, the first batch was laid *c.a.* 12.5 to 20 months (393-588 days) from hatching (mean=466 days; SD=106.33; n=3).

Growth that includes both slow and fast phases has been observed in some helicoids [28,36]. In *Perforatella*

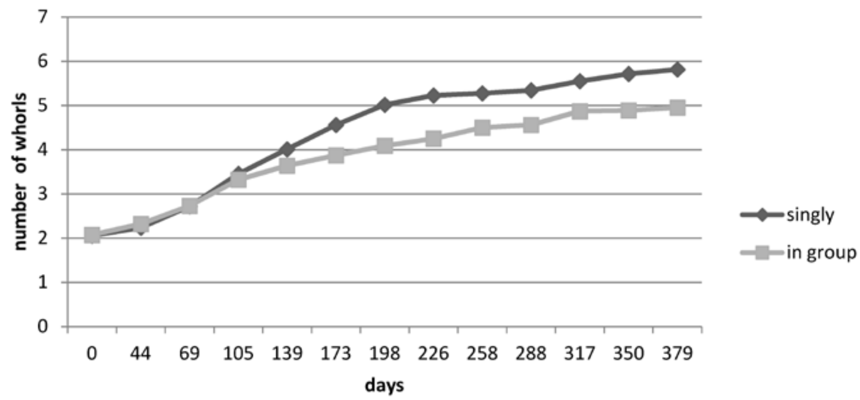

Figure 2. Average growth of *B. fruticum* kept singly and in a group, (n=10, for each case).

bidentata and *Trochulus hispidus*, the fast phase included the period from hatching to about 5 whorls, and the slow phase occurred beyond 5 whorls. The growth of *B. fruticum* included two slow phases (from hatching to 2.25 whorls and after reaching 5.0 whorls) as well as one fast phase (2.25 to 5.0 whorls). Growth in the laboratory was slightly faster than in the field [13], both during the slow (0.14 and 0.10 whorl/month, respectively) and the fast phase (0.57 and 0.44 whorl, respectively). Potential reasons for these differences include more favourable and stable conditions of humidity, temperature and food availability in the laboratory, but the observed growth rates are generally similar.

In a study by Staikou *et al.* [5] *B. fruticum* reached morphological maturity 21 months after hatching, when the largest shell diameter exceeded 19.3 mm. In contrast, Frömming [37] and Bába [4] reported sexual maturity at 13-14 months after hatching and a shell height of 12-14 mm. Our observations showed that, in the laboratory, lip formation occurred sooner, 9 to 13 months from hatching, at a shell width of 15.89-18.17 mm. These differences may result from different environmental conditions. Frömming [37] maintained that maturation of *B. fruticum* kept in the laboratory was delayed. In the laboratory, *B. similaris* reached maturity as soon as *c.a*. 2.5-6 months [15].

The growth rate of individuals of *B. fruticum* kept in isolation and in a group differed. When they reached *c.a.* 3.4 whorls, the snails kept in a group showed a much lower growth rate compared to snails kept singly. Besides, none of the individuals kept in a group formed a lip while the single snails reached morphological maturity in 10-12 months. A similar tendency was observed in the laboratory studies on *B. similaris*: after a time isolated individuals started growing much faster than those kept in a group, and reached a greater shell width. However, the snails kept in groups were quicker to form lips (minimum time from hatching to lip formation 2.5 months, compared to individuals kept singly – 3.5-6.5 months) [15]. Similar differences in growth rate were observed for *Alinda biplicata*, where the time needed to reach adult size increased with increasing snail density [38].

In land snails two types of strategies can be distinguished depending on the allocation of resources. The first type involves the investment of all resources into growth; once the individual reaches its ultimate size, it stops growing and invests all reserves into reproduction. In snails showing the second strategy, growth continues in mature individuals, practically until death [39; for examples and a litertaure review, see 40-44]. Although *B. fruticum* continued growing after lip completion in the laboratory, growth increments were very small in adults compared to juveniles. In the field, no changes in the adult shell size were observed [13]; a similar situation was described in *Helicodonta obvoluta* [27]. These observations suggest that *B. fruticum* employs the first type of growth strategy. A similar growth pattern was observed in *B. similaris* [16].

According to Staikou *et al.* [5], mortality in *B. fruticum* was very small during the first year of its life and increased with age to reach its maximum after attainment of sexual maturity. In our study, many snails died having reached *c.a*. 3.4 whorls. Mortality also ncreased with snail density. We did not notice increased mortality among sexually mature *B. fruticum*. On the contrary, most of the observed deaths took place prior to the snails attaining maturity.

3.3 Life span

Among the 18 individuals of the first generation (offspring of the snails collected in the field in June

2009), seven were still alive on 6.04.2011. The life span of these seven snails was 352-626 days (mean=433.09; SD=68.86, n=11); three of them died before lip formation. Among 50 snails of the second generation hatched between 13.03.2010 and 29.03.2010, the 10 that we isolated were still alive on 6.04.2011. The life span of the remaining 40 (kept in four containers with 10 snails each) ranged from 141.4 to 395.0 days (mean=235.17; SD=75.79; n=20).

The life span of *B. fruticum* in the laboratory ranged from 352 to 626 days. The snails reached a similar number of whorls in the laboratory and in the field [13]. The maximum number of whorls in *B. fruticum* raised in the laboratory was 6.1 compared to 6.0 in the wild. In northern Greece, Staikou *et al*. [5] observed that *B. fruticum* needed 5 years to reach its maximum size (shell width 25.4 mm) in the wild. The largest individual in our laboratory culture was about 2.5 years old and had a shell width of 18.17 mm when it completed its growth. A relatively short life span combined with large reproductive output was observed by other authors in both *B. fruticum* [5] and *B. similaris* [16]. Their life strategies were assigned to type r.

3.4 Circadian activity

The circadian activity of juveniles and adults is presented in Figure 3. Juvenile snails were much more active than adults in the spring, summer and autumn. In the winter, adults were much more mobile. Juveniles were more mobile than adults at night, irrespective of the season. Activity patterns were similar in all seasons except during autumn when snails were less active. We found no relationship between activity patterns and temperature during our study.

Acknowledgements

We thank Dr. Anna Sulikowska-Drozd for her critical and detailed remarks on the manuscript. We are also grateful to an anonymous reviewer for helpful comments.

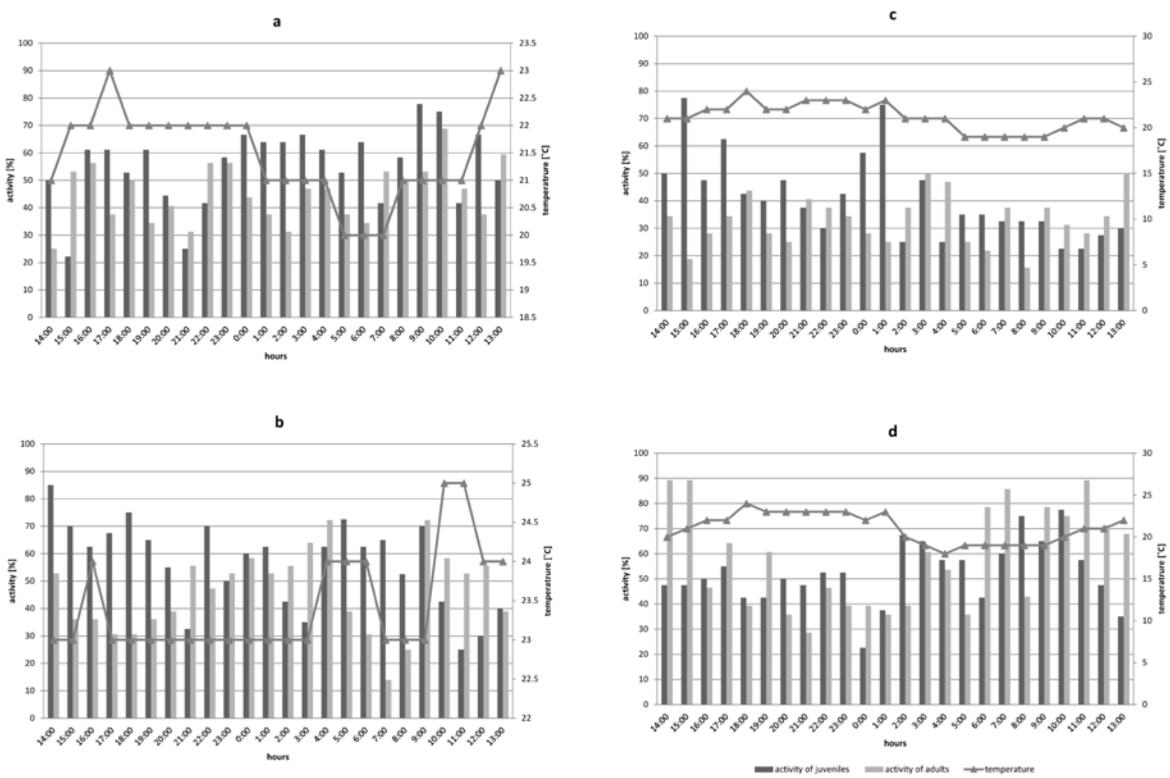

Figure 3. Diurnal activity patterns of juvenile and adult *Bradybaena fruticum*: a - spring, b - summer, c - autumn, d - winter.

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