POPULATION DYNAMICS OF THE CARPATHIAN CLAUSILIID *VESTIA GULO* (E. A. BIELZ 1859) (PULMONATA: CLAUSILIIDAE) UNDER VARIOUS CLIMATIC CONDITIONS

Anna Sulikowska-Drozd

Department of Invertebrate Zoology and Hydrobiology, University of Łódź, Banacha Str. 12/16, 90–237 Łódź, Poland

Abstract *Population dynamics of the hygrophilous, egg-retaining clausiliid* Vestia gulo *was studied in the Carpathians (Poland) over three years at four sites that differ in their temperature regime. Juveniles (2.5 whorls) hatched in late June and/or in July. At the highest located site (1150 m a.s.l.) juveniles reached 3.5–4 whorls in the first growing season, 5.5–7 in the second, and probably attained maturity in the third or fourth season of their life (shells with 8.3–10.1 whorls). At the intermediate site (759 m a.s.l.), snails reached 4.0–6.0 whorls in the first growing season, 7.4–9.4 in the second and completed growth with 9.0–11.25 whorls at the third growing season. At two lowest sites (both at 425 m a.s.l.) populations of* Vestia gulo *differed in the growth rate, consequently snails reached ultimate size in two or three seasons. In the fastest growing population in the first season juveniles grew to 5.5–8.4 whorls, then during the second growing season they reached the ultimate size (9.25–12.25 whorls). Marked adults lived at least four years. Copulations were observed in autumn; in winter, there was hardly any growth.*

Key words *life-history, longevity, growth rate, land snails, Clausiliidae*

Introduction

Life histories of terrestrial pulmonates exhibit substantial variability induced by environmental factors (Baur & Raboud, 1988; Heller, 2001) but which also may be explained by genetic differences between populations (Jordaens *et al.*, 2006). Intraspecific differences in life histories were described in some helicids: *Theba pisana* (Cowie, 1984), *Arianta arbustorum* (Baur & Raboud, 1988), *Xeropicta derbentina* (Kiss *et al.*, 2005), and *Xerolenta obvia* (Lazaridou & Chatziioannou, 2005), and vitrinids: *Semilimax kotulae*, *Vitrina pellucida,* and *Eucobresia nivalis* (Umiński, 1975). It was found that temperature and humidity pattern governs the length of activity and growth rate, thus shaping the size structure and dynamics of local populations (Umiński, 1975; Oosterhoff, 1977; Terhivuo, 1978; Cowie, 1984). Peake (1978) suggested that the degree to which the life history strategies can vary with climate is an important factor in determining the distribution and success of the species, yet this variation tends to be ignored or underestimated in land snails.

The aim of this paper is to show the differences in life history of four populations of clausiliid *Vestia gulo* (E. A. Bielz 1859), the reproductive biology of which was previously studied under laboratory conditions (Sulikowska-Drozd, 2009). The species is ovoviviparous *sensu lato* – it retains developing eggs in its reproductive tract. The eggs are laid in batches, which usually consist of 11–15 eggs, and hatch after 8–10 days of incubation (temp. 20°C). Neonates (shells with 2.5 whorls, ca. 2 mm in length) need at least 3.5–4 months to complete shell growth and an additional 5–6 months to lay eggs (Maltz & Sulikowska-Drozd, 2008).

Vestia gulo is distributed in the Carpathians and Transylvania over a range of ca. 1,000 m elevation range (the highest localities at 1,300 m a.s.l.) (Riedel, 1988; Sulikowska-Drozd, 2005). It was hypothesised that various temperature regimes of the mountain sites (associated with altitude, exposition, relief and habitat type) were the factors responsible for variation in its life history characters, as the species occurs only in spring areas or in shrubs/forests on stream banks, where humidity is high and stable throughout the year (Sulikowska-Drozd, 2005).

Methods

Data were collected in the Pieniny Mts. & Gorce Mts. (S Poland) in the years 2005–2007 (Fig. 1). Seasonal changes in size distribution of *Vestia gulo* populations were observed at four sites in the foothills, middle mountain zone and upper mountain zone. The main characteristics of the sampling sites are given in Table 1. Sampling started in April 2005 at station RZ, and in the

Contact author : sulik@biol.uni.lodz.pl

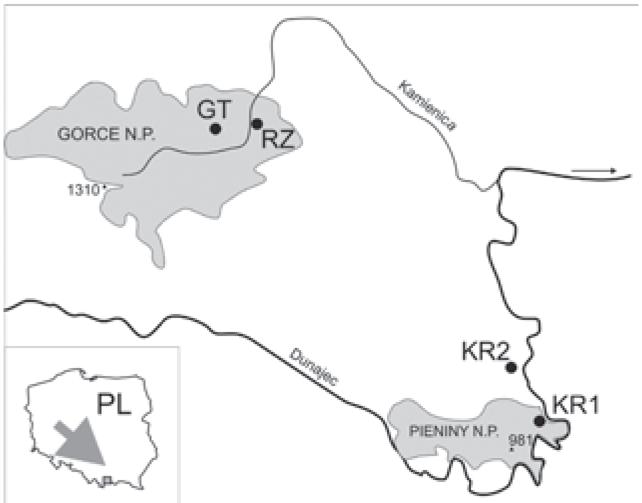

Figure 1 Study area in the Carpathian Mts, with sampling stations in Krościenko (KR1 & KR2), Rzeki (RZ) and Gorc Troszacki (GT).

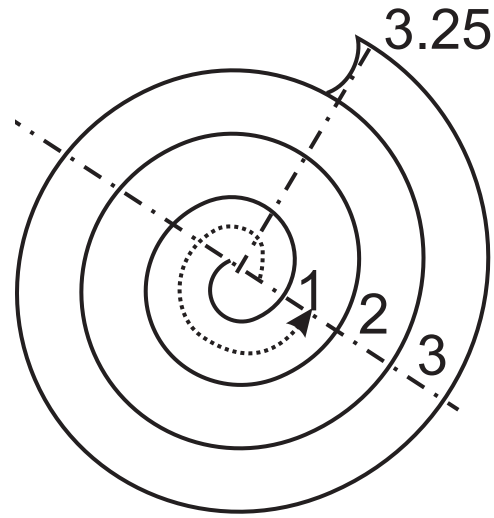

Figure 2 Method of whorl counting.

following months at stations KR2 and KR1. To widen the altitudinal range of sampled population the fourth station (GT) was added in July 2006. Each population was sampled 6–12 times. For logistic reasons snails could not be collected at regular intervals, but in the analysis the exact number of days between consecutive sampling was taken into consideration. Sampling frequency was the highest in the growing period 2006 (samples every 4–4.5 week).

Snails were sampled by visual search from the same area (2–3 m) each time. The sampling took at least 3 hours at each site. The quantitative sampling by square–frame method was rejected here to avoid the destruction of vegetation and soil and because it may underestimate the density (Baur, 1986; Oggier *et al.*, 1998). For each snail the shell height was measured with slide callipers (accuracy 0.1 mm) and the number of whorls was counted to nearest 0.1 whorl as shown in Fig. 2. Adult shells with thickened, everted lip were measured only once when the snail was collected for the first time. Shells were marked with nail-varnish (each time a different colour). The marks for juvenile specimens were painted on the penultimate whorl, just above the palatal

Table 1 Sampling sites; habitat characteristics.

	Sampling sites			
	KR 1	KR 2	RZ	GT
Locality	Krościenko – Ociemny	Krościenko – near sewage plant	Rzeki – near „Papieżówka"	Gorc Troszacki
Geographical area	Pieniny Mts	Gorce Mts	Gorce Mts	Gorce Mts
Altitude a.s.l.	425 m	425 m	759 m	1150 m
Slope	0–5%	0–10%	5–10%	5–10%
Exposition	E	E	W	N
Coordinates	N 49°25′52.8″ E 020°26′14.0″	N 49°25′57.7″ E 020°25′17.0″	N 49°34′21.3″ E 020°13′10.8″	N 49°34′29.3″ E 020°11′36.6″
Habitat type	Submontane zone	Submontane zone	Lower mountain forest zone	Upper mountain forest zone
Plant community	Alder swamp/ eutrophic meadow	Alder swamp/ anthropogenic habitat	Alder swamp	Spring area in spruce forest
Canopy	60%	30%	70%	70%
Herb layer	100%	60%	60%	60%
Soil pH	7.5	8.15	6.7	7.4

Table 2 Temperature records from the studied sites (1 Nov. 2006–25 Sept. 2007).

	KR1	RZ	GT
Temperature (°C)			
Mean	7.68	6.08	5.16
Minimal	−8.22 (27 Jan)	−7.34 (27 Dec)	−4.05 (27 Jan)
Maximal	24.6 (20 July)	23.6 (20 July)	18.30 (20 July)
No. of days with mean temp.			
>5°C	190	162	141
>15°C	67	31	3
<0 °C	109	118	37

Table 3 *Vestia gulo*. Adult shell height and whorl number in studied populations; n – number of specimens.

	Station	n	Mean	SD	Min-Max
Number of whorls	KR1	1238	10.60	0.40	9.50–12.25
	KR2	750	10.67	0.39	9.25–11.75
	RZ	655	10.13	0.37	9.00–11.25
	GT	182	9.40	0.32	8.30–10.10
Shell height (mm)	KR1	1238	16.25	0.73	14.1–18.8
	KR2	750	16.52	0.77	11.8–19.2
	RZ	655	15.59	0.64	13.8–17.6
	GT	182	14.43	0.55	12.2–16.1

margin of the aperture; for adults, close to the palatal side of the aperture. Afterwards the snails were released. During consecutive sampling each re-captured individual was measured and the shell increment since the previous markings was estimated. In 2008 and 2009 each site was searched for the presence of living individuals which were marked during the period of study.

The data were used to draw size-distribution diagrams for the studied populations. Growth rate was estimated on the base of the difference in whorl numbers encountered during the successive dates of recapture. The differences in shell growth between populations at KR2 and RZ, which were observed for the longest period, were tested (Mann-Whitney U test). The adult shell height and the number of whorls was compared among studied populations with ANOVA and *post-hoc* Tukey test.

At three sampling sites (KR1, RZ, GT) the temperature was recorded automatically every two hours by means of Tinytag data loggers (Gemini data logger) from November 2006 to October 2007 (330 days). The sensors were put under tree logs, ca. 10 cm above ground, within each sampling site. Temperature records are summarized in Table 2.

RESULTS

At the sampling sites 8605 *Vestia gulo* specimens were collected and marked; 1618 were recaptured. Adults from the studied populations exhibit statistically significant interpopulation variation in shell height ($F (3, 2821) = 542.44$; $P<0.0001$) and number of whorls ($F (3, 2821) = 729.00$; $P<0.0001$). The differences are significant among all studied populations (post–hoc T tests: $P<0.001$). The largest shells were found in populations from foothills (KR1 and KR2) – the mean numbers of whorls were 10.6 and 10.7, respectively; mean shell heights were 16.25 and 16.52 mm (Table 3). The smallest were found in the upper mountain zone (GT) with a mean number of whorls of 9.4 and a mean shell height of 14.4 mm. In the population from the lower mountain zone (RZ) the shell size was intermediate (mean number of whorls 10.1; mean shell height 15.6 mm).

The seasonal changes in size distribution in the studied populations are shown in Fig. 3. At KR1 the population, first encountered in autumn (September 2005), consisted of three groups: adults and two groups of juveniles. By late autumn the smaller juveniles grew and reached 5.0–7.0 whorls and the group of bigger juveniles did not grow much and they stayed the same. During winter growth was very slow (maximum 0.5 whorl per seven months) (Fig. 4).

In the next spring-summer season, growth was faster (juveniles grew up to 2.1 whorls per month) and bigger juveniles attained adult size: the proportion of shells with everted lips increased in the population. Juveniles from the second group also grew and reached 8.0–10.0 whorls and overwintered for the second time as juveniles. Also in this summer a new generation appeared, that grew to 4.4–5.4 whorls by the end of autumn.

At the onset of the third season (April 2007) there were, once again three size groups: adults,

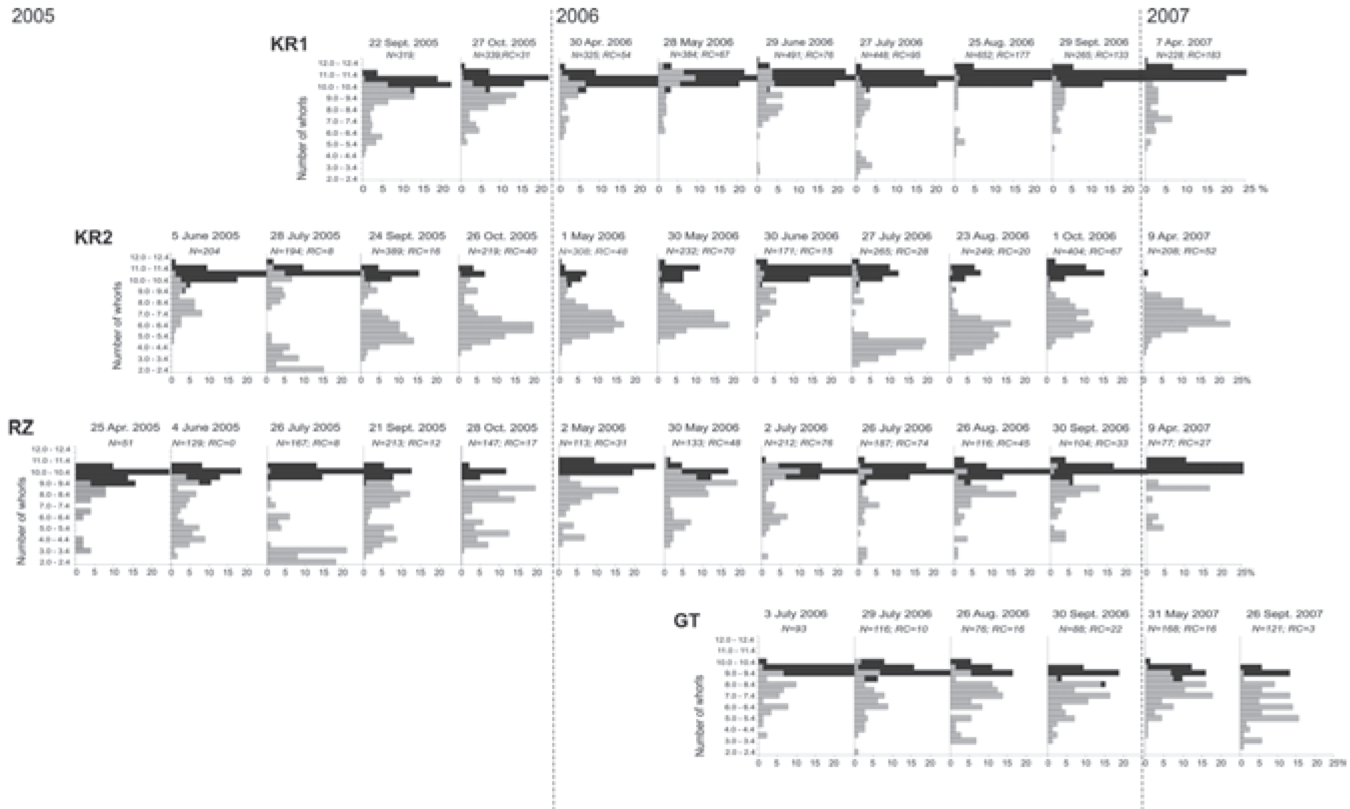

Figure 3 Size distribution of *Vestia gulo* (by whorl number) at four sampling sites (light grey – juveniles; dark grey – adults; N – number of collected snails; RC – number of recaptured snails).

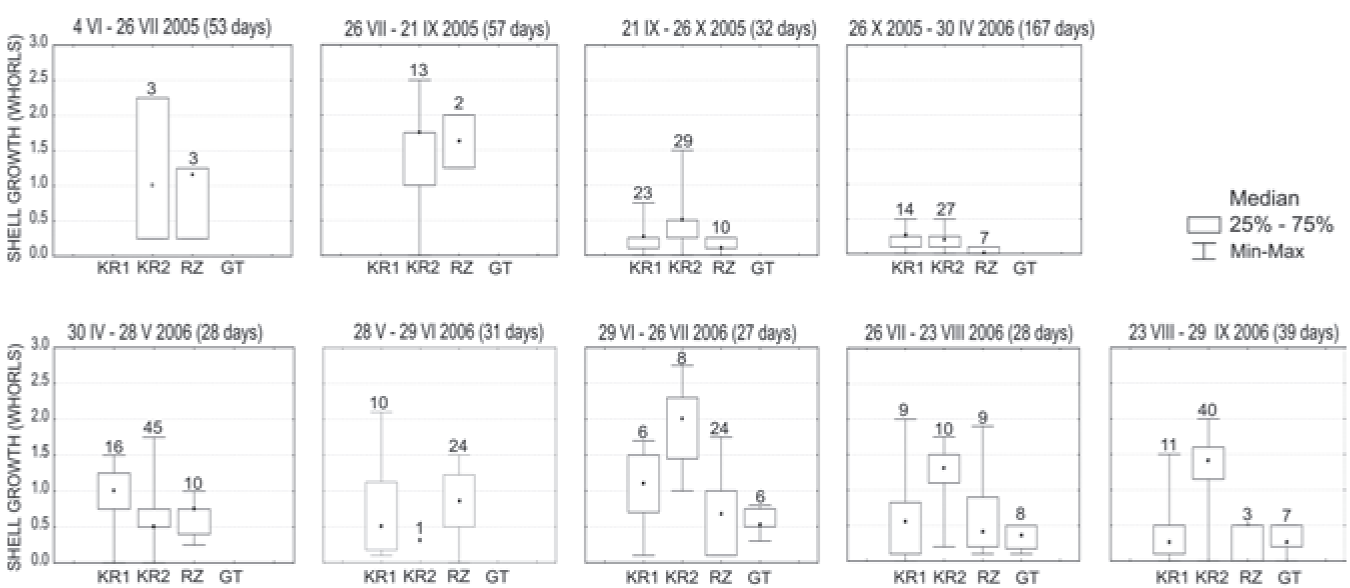

Figure 4 Shell growth of *Vestia gulo* juveniles – whorl increment between sampling occasions. Numbers over the whiskers indicate the number of recaptured juveniles.

juveniles that had hatched two seasons ago (almost of adult size) and a group of juveniles born one season ago.

At KR1 growth of snails was fairly rapid (an average 4.1 whorls and maximum 8.0 whorls per growing season) but it appears that only a

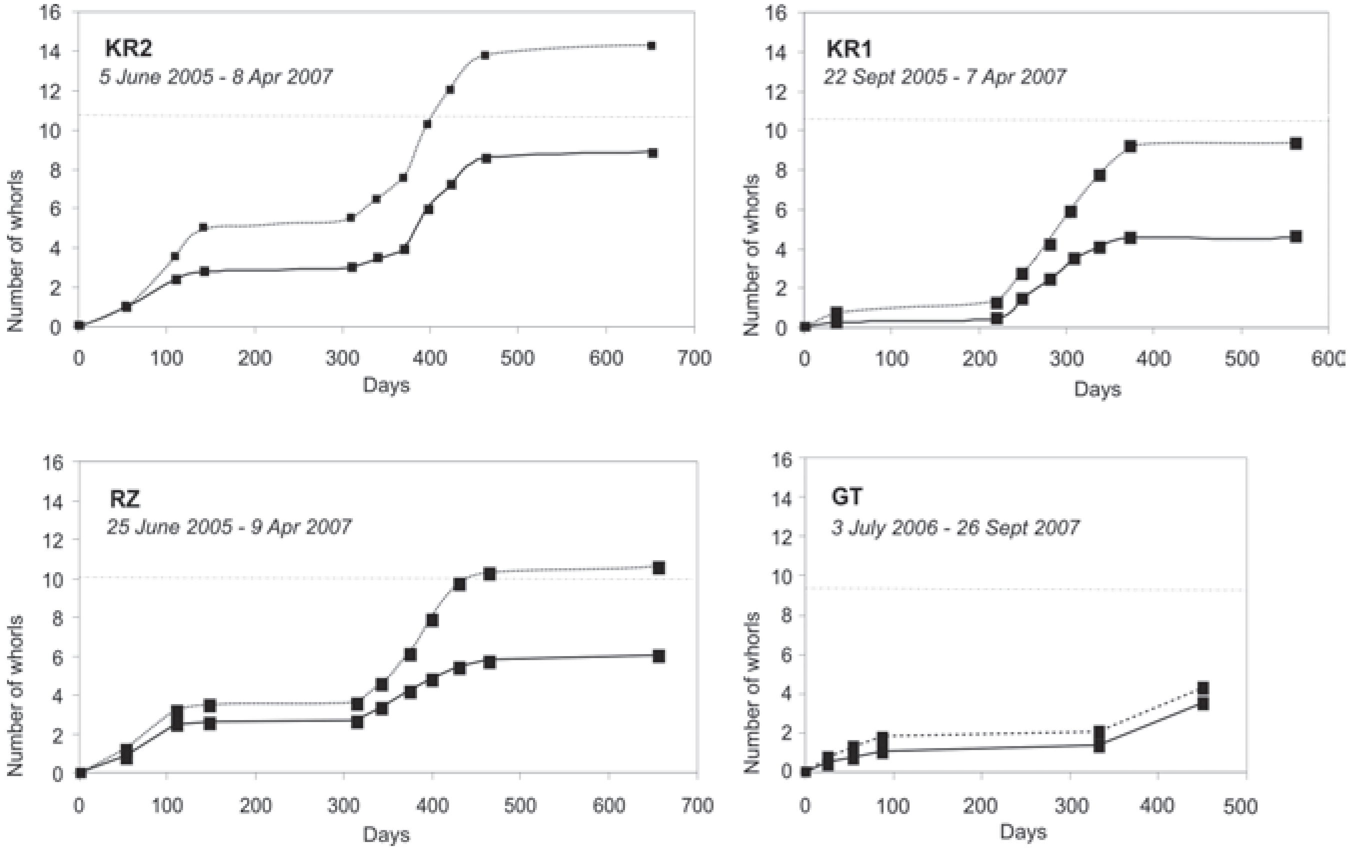

Figure 5 Growing curves of *Vestia gulo* at the studied sites. Solid line – average whorl increment; dotted line – maximum whorl increment; horizontal line – the average number of whorls in adults; black squares – records for sampling occasions.

small proportion of juveniles may reach their ultimate size in two seasons, while the majority need three seasons to complete shell formation (Fig. 5).

At KR2 the population first encountered in summer 2005 (June), consisted mainly of juveniles that were crawling about on the very moist ground or on stones on the bank of a small brook, or on stems of *Petasites* sp. The population included a group of adults, and two groups of juveniles (6.0–8.4 whorls and 9.0–10.4 whorls). During summer the bigger juveniles reached the adult size and the smaller grew to 9.4–10.0 whorls. A new generation appeared in the summer (July) and grew rapidly until, by autumn, it reached a size of 5.5–6.5 whorls.

In the following spring and summer (May–June 2006) the group of bigger juveniles merged into the adult group. By autumn (October 2006) the juveniles born in 2005 also reached the ultimate size. In mid summer (July 2006) a new generation appeared and it grew rapidly reaching the size of 5.0–8.4 whorls.

In the spring of the following, third season (April 2007) there were adults and juveniles born in the summer of one season ago.

These observations are supported by the results of recapture of marked juveniles. During the 2006 growing season, the average growth of juveniles equalled 5.3 whorls, while the maximum was 8.5 whorls (Fig. 5). The fastest growth occurred in July – the maximum recorded value was 2.75 whorls/month (Fig. 4). In winter months, the maximum whorl increment was small (0.5 whorls from late October 2005 to early May 2006 and 1.5 whorls from early October 2006 to early April 2007).

At RZ the population, first encountered in spring (April 2005), consisted of adults and two groups of juveniles (small, 3.0–4.4 whorls and big, 7.4–9.4 whorls). By summer some of the latter group of juveniles achieved adult size and by autumn (October 2005) the group of smaller juveniles grew to 7.0–9.4 whorls. In summer (July 2005) a new generation appeared and started growing so that by autumn they reached 3.4–6.0 whorls.

In the second season, during summer the group of now bigger juveniles merged into the adult size group (May-July 2006) and the new generation of 2005 continued growing so that by autumn (September 2006) it reached 7.4–9.4 whorls. A new cohort appeared during summer (July 2006) and grew considerably, so that by autumn (September 2006) it had reached 4.4–5.4 whorls.

In the spring of the following, third season (April 2007) there were adults; a cohort of bigger juveniles (born in summer of two season ago) and smaller juveniles (born in the summer of one season ago).

Based on the whorl increment of recaptured individuals the growth of snails was very slow between late October and the beginning of May (maximum growth 0.1 whorl per six months). In June–August growth was more rapid; maximum 1.5–1.9 whorls/month (Fig. 8). During the whole growing season 2006 the average increment was 3.0 whorls, while the maximum was 6.6 whorls.

In the population at GT, first encountered in summer (July 2006), there were adults and two ill defined groups of juveniles. A new generation hatched in late July and reached the size of 3.5–4 whorls in the first growing season. In the following season juveniles grew only 2–3 whorls. Thus, snails overwintered at least twice as juveniles, but most probably three times, before the growth was completed.

Shell growth rate was compared between populations KR2 and RZ (Mann-Whitney U test). It was slower at RZ site than at KR2 site during autumn 2005 and summer 2006, while in summer 2005 and early spring 2006 the differences were not significant (Table 4).

Additional findings concern copulation and egg laying. In spite of long visits on the sampling sites copulation of *V. gulo* was rarely observed during the study period. Single pairs were noticed at KR1 in autumn (2 Sept. 2006, 29 Sept. 2006, 6 Oct. 2007, 12 Oct. 2008, 10 & 14 Oct. 2009). In June and July, the eggs of *Vestia gulo* were found under bark (station – RZ) and in mosses (station – KR2).

Specimens, of *V. gulo* marked in October 2005 as adults at stations KR1 and RZ, were found alive in September 2009. Thus they lived at least four years as adults. At the GT station, snails marked in 2006 were found in 2008 (at least two years of adult life). There are no data on longevity of snails from KR2. That population was much reduced by a flood on 10 June 2007 and finally disappeared in summer 2008 during road construction.

Table 4 Comparison of *Vestia gulo* shell growth between two consecutive markings at stations RZ and KR2; n.s. – not significant.

	Shell growth (number of whorls) median KR2	Shell growth (number of whorls) median RZ	Mann-Whitney U test
4–5 VI – 26–28 VII	1	1.15	n.s.
26–28 VII – 21–24 IX	1.75	1.625	n.s.
21–24 IX – 26–28 X	0.5	0.1	P=0.003
26–28 X – 1–2 V	0.2	0	P=0.002
1–2 V – 30 V	0.5	0.75	n.s.
30 V – 30VI–2VII	0.3	0.85	n.s.
30VI–2VII – 26–27 VII	2.0	0.675	P=0.0000
26–27 VII – 23–26 VIII	1.3	0.4	P=0.028
23–26 VIII – 30 IX-1 X	1.4	0.5	P=0.002

DISCUSSION

Temperature differences at studied sites The altitudinal difference of 700 m between KR1/KR2 and GT in the Gorce Mts. implies significant climatic diversity. As *Vestia gulo* inhabits only places with constant high humidity, the observed variation in life history should be attributed mainly to the temperature regime at each site. The temperature data presented in Table 3 confirm the general climatic pattern of the Carpathian Mts. with a constant decrease in temperature from lower to upper mountain zones (Obrębska-Starklowa *et al.*, 1995). During 11 months (1 Nov. 2006–25 Sept. 2007) the mean temperature at the highest located station (GT) was 2.5°C lower than at the foothills (KR1). The number of days with mean temperature >5°C was 141 at the GT station and 190 at the KR1 station. The number of days with a mean temperature >15°C (climatic summer) was 3 and 67, respectively. At the RZ station, located at a low altitude but in a deep, north-facing valley, the mean temperature was intermediate. At the highest station (GT) the number of frosty days was low due to thick snow cover (at least 70–80 cm) which persisted to the middle of April (personal observation, 2007). Under the snow the ground was heated by spring water which in the upper mountain zone of the Gorce Mts had a temperature of 4–7°C throughout the year (Chaniecka, 2002). Ground frost occurred most frequently at station RZ and KR1, where snow cover was thinner and melted during warmer periods in winter.

Reproduction and population dynamics In natural populations of *Vestia gulo* the reproductive season (egg laying and hatching) is in late spring-early summer. The occurrence of a single reproductive season in *V. gulo* was confirmed by anatomical investigation of its reproductive tract. Eggs/embryos were found in uterus from the middle of May to the end of July (one case in October), but the first advanced embryos (with embryonic shell >1 whorl) occurred at the end of May (Sulikowska-Drozd, 2009). In autumn snails mate but during winter months no embryos were found in oviducts. Under laboratory conditions, in stable temperature and humidity, the species did not cease reproduction in winter (unpublished data). Some other clausiliid species inhabiting Central Europe have a second reproductive period in autumn, however eggs always hatch before winter (Piechocki, 1982; Bulman, 1998). In the Mediterranean region, the reproductive season of clausiliids is strictly correlated with the first autumn rain (Heller & Dolev, 1994, Giokas & Mylonas, 2002). In *Albinaria* copulation occurred immediately after synchronous awakening from aestivation, while egg laying and hatching lasted through the first month of the wet period in dry regions, or continued through active period in more humid sites (Giokas & Mylonas, 2002).

In this study populations of *V. gulo* differed in terms of growth rate depending on the temperature regime of a site to such an extent that the pre-reproductive phase of life may last 1–4 years. Similar variation was observed in *Arianta arbustorum* populations in the Alps (Baur & Raboud, 1988). Snails from a population at 1,220 m a.s.l. matured after 1.9 years while another at 2,600 m only after 5 years, although adults from each population lived 3–3.5 years. Thus, the total lifespan lengthens as altitude increases. Baur and Raboud (1988) found that most life-history traits correlated with the thermal regime of the locality. Snails from the highest localities laid smaller eggs, in smaller batches; oviposition was less frequent and overall reproductive effort during a lifetime was lower. Experiments with snails transplanted from summit localities to valley localities showed that some traits, such as the size and weight of egg batches, and growth rate, did not change as a consequence of transplantation, while the frequency of oviposition increased and the onset of reproduction was earlier. On the northern periphery of its range *A. arbustorum* needs 3–4 years to attain maturity, which was attributed to a shorter activity period in comparison with Central Europe (Terhivuo, 1978).

In *Vestia gulo* significant differences in growth rate were observed between populations inhabiting elevations which differed by 250 m. Similarly, Umiński (1975) found that *Vitrina pellucida* and *Semilimax kotulae* had a one-year cycle at 980 m a.s.l. and a two-year cycle at 1,240 m in the Tatra Mts. In the Mediterranean region humidity rather than temperature is the major factor in life history variation. According to Lazaridou & Chatziioannou (2005), populations of *Xerolenta obvia* in northern Greece had a one- or two-year life cycle depending on the precipitation: the number of eggs in a batch and the size of eggs also varied.

Besides climatic factors the growth rate and adult size in land snails is influenced by population density (Oosterhoff, 1977; Baur, 1990; Cook, 2001). Baur & Baur (1990) showed by experiment that juvenile growth rate, time to complete growth, adult shell size and survival were significantly influenced by the density of conspecifics in the clausiliid *Balea perversa.* Similarly, growth of juveniles to adulthood was probably inhibited in natural population of *Cristataria genezarethana* by the presence of already mature animals via their deposition of mucus (Heller & Dolev, 1994). Cook (2001) showed that the effect of mucus on activity and growth in laboratory conditions persisted even when food was provided *at libitum*, while the complex interaction occurring in the field needed more careful interpretation. The population density of *Vestia gulo* was not estimated in this study, but in other forest habitats in the East Carpathians it ranged from 3 to 49 specimens/m (Sulikowska-Drozd & Horsak, 2007). Preliminary data obtained by square–frame sampling at KR1 showed the very high density of 475 specimens/m (Sulikowska-Drozd, unpublished). It may explain the slower growth of snails here in comparison with the population at KR2.

Clausiliids are long-lived (Piechocki, 1982; Heller & Dolev, 1994). In this study *V. gulo* lived at least four years of adult life and the time of growing lasted one year in a submontane zone and 3–4 years in the upper mountain zone. These results are in concordance with previous data on the congeneric species *V. elata*. Piechocki (1982) showed that marked specimens of *V. elata* lived at least 8 years, with two years of growing. *Cristataria genezarethana* takes up to 11 years to reach maturity due to short activity periods during wet season Heller & Dolev (1994).

Shell size variation Arianta arbustorum in the Alps provides the best studied example of variation in shell size along an altitudinal gradient (Burla & Stahel, 1983; Baur, 1984). As in that case, *V. gulo* decreased in size with increasing altitude, as does the congeneric *V. turgida* (Sulikowska-Drozd, 2001). Goodfriend (1986) noted the association of particularly small forms with high elevation in his general review of shell form in land snails, but did not discuss the life-history implication of that pattern. Elsewhere it was suggested that because summers are short at high altitudes, selection might favour neoteny (Burla & Stahel, 1983). In clausiliids it may imply formation of the ultimate whorl with clausilium and attaining reproductive maturity at the relatively small size. In contrast, in the Vitrinidae, with indeterminate growth, shell size tends to reach a large size at higher altitudes as a consequence of increased life span (Umiński, 1975).

Finally, it should be noted that splitting of specimens into adult and juvenile groups was based here on conchological criteria. This could overestimate the number of reproductively active snails in a population. It was found in some species in the genus *Albinaria* that there was a time lag between the completion of shell growth and sexual maturity (Schilthuizen & Lombaerts, 1994, Giokas & Mylonas 2002). Snails which finished their growing in spring were unable to reproduce during the following few months, as the shell development was faster than reproductive maturity, which occurred during summer aestivation. The growing pattern in *Vestia gulo* is similar. It was found that 2–3 months after lip formation reproductive tracts are still underdeveloped and there are only a few mature oocytes in a gonad (Maltz & Sulikowska-Drozd, in prep.). It seems that snails which completed shell growth in late summer do not reproduce in the same growing season, or they are able to copulate but do not lay eggs. In Vitrinidae, with indeterminate growth, there is no direct relationship between size and reproduction (Umiński, 1975).

Acknowledgements

Sampling in protected areas was permitted by the authorities of Gorce National Park and Pieniny National Park, to whom I am indebted. I am also very grateful to everyone who accompanied me on the field work, especially to Monika Kuna, MSc. The project was supported by grant 2P04C 029 30 from the State Committee for Scientific Research.

References

Baur A 1990 Intra- and inter-specific influences on age at first reproduction and fecundity in the land snail *Balea perversa*. *Oikos* **57**: 333–337.

Baur A 1984 Shell size and growth rate differences for alpine populations of *Arianta arbustorum* (L.) (Pulmonata: Helicidae). *Revue suisse de Zoologie* **91**: 37–46.

Baur A 1986 Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). *Holarctic ecology* **9**: 117–125.

Baur B & Baur A 1990 Experimental evidence for intra-and interspecific competition in two species of rock-dwelling land snails. *Journal of Animal Ecology* **59**: 301–315.

Baur B & Raboud CH 1988 Life history of the land snail *Arianta arbustorum* along an altitudinal gradient. *Journal of Animal Ecology* **57**: 72–87.

Bulman K 1998 Age structure of *Cochlodina laminata* (Gastropoda: Clausiliidae). *In* Bieler R & Mikkelsen PM (eds) *Abstracts, World Congress of Malacology, Washington, DC:* 47. Unitas Malacologica.

Burla H & Stahel W 1983 Altitudinal variation in *Arianta arbustorum* (Mollusca, Pulmonata) in the Swiss Alps. *Genetica* **62**: 95–108.

Chaniecka K 2002 *Makrobezkręgowce (Macro-invertebrata) obszarów źródliskowych Gorczańskiego Parku Narodowego.* Ph.D thesis, University of Lodz, Lodz.

Cook A 2001 Behavioural Ecology: On Doing the Right Thing, in the Right Place at the Right Time. *In* Barker GM (ed.) *The Biology of Terrestrial Molluscs:* 447–487. CABI Publishing, Wallingford.

Cowie RH 1984 The life cycle and productivity of the land snail *Theba pisana* (Mollusca: helicidae). *Journal of Animal Ecology* **53**: 311–325.

Giokas S & Mylonas M 2002 Spatial distribution, density and life history in four *Albinaria* species (Gastropoda, Pulmonata, Clausiliidae). *Malacologia* **44**: 33–46.

Goodfriend GA 1986 Variation in land-snail shell form and size and its causes: a review. *Systematic Zoology* **35**: 204–233.
Heller J 2001 Life History Strategies. *In* Barker GM (ed.) *The Biology of Terrestrial Molluscs*: 413–445. CABI Publishing, Wallingford.
Heller J & Dolev A 1994 Biology and population dynamics of a crevice-dwelling landsnail, *Cristataria genezarethana* (Clausiliidae). *Journal of Molluscan Studies* **60**: 33–46.
Jordaens K, Pinceel J & Backeljau T 2006 Life-history variations in selfing multilocus genotypes of the land slug *Deroceras leave* (Pulmonata: Agriolimacidae). *Journal of Molluscan Studies* **72**: 229–233.
Kiss L, Labaune C, Magnin F & Aubry S 2005 Plasticity of the life cycle of *Xeropicta derbentina* (Krynicki, 1836), a recently introduced snail in Mediterranean France. *Journal of Molluscan Studies* **71**: 221–231.
Lazaridou M & Chatziioannou M 2005 Differences in the life histories of *Xerolenta obvia* (Menke, 1828) (Hygromiidae) in a coastal and a mountainous area of northern Greece. *Journal of Molluscan Studies* **71**: 247–252.
Maltz TK & Sulikowska-Drozd A 2008 Life cycles of clausiliids of Poland – knowns and unknowns. *Annales Zoologici* **58**: 857–880.
Obrębska-Starklowa B, Hess M, Olecki Z, Trepińska J & Kowanetz L 1995 Klimat. *In* Warszyńska J (ed.) *Karpaty Polskie. Przyroda, człowiek i jego działalność:* 31–47. Uniwersytet Jagielloński, Kraków.
Oggier P, Zchokke S & Baur B 1998 A comparison of three methods for assessing the gastropod community in dry grasslands. *Pedobiologia* **42**: 348–357.
Oosterhoff L 1977 Variation in growth rate as ecological factor in the land snail *Cepaea nemoralis* (L.). *Netherlands Journal of Zoology* **27**: 1–132.
Peake J 1978 Distribution and Ecology of the Stylommatophora. *In* Fretter V & Peake J (eds) *Pulmonates 2A: Systematics, Evolution and Ecology*: 429–526. Academic Press, London.
Piechoki A 1982 Life cycle and breeding biology of *Vestia elata* (Rossm.) (Gastropoda, Clausiliidae). *Malacologia* **22**: 219–223.
Riedel A 1988 Ślimaki lądowe. *Gastropoda terrestria*. Katalog Fauny Polski **36**. 316 pp.
Schilthuizen M & Lombaerts M 1994 Population structure and levels of gene flow in the Mediterranean land snail *Albinaria corrugata* (Pulmonata: Clausiliidae). *Evolution* **48**: 577–586.
Sulikowska-Drozd A 2001 Shell variability in *Vestia turgida* (Rossmässler, 1836) along an altitudinal gradient. *Folia Malacologica* **9**: 73–81.
Sulikowska-Drozd A 2005 Distribution and habitat preferences of clausiliids (Gastropoda: Pulmonata: Clausiliidae) in the eastern part of the Polish Carpathians, *Folia Malacologica* **13**: 49–94.
Sulikowska-Drozd A 2009 Egg-retention and ovoviviparity in clausiliids of the genus *Vestia* P. Hesse (Gastropoda: Clausiliidae). *Journal of Molluscan Studies* **75**: 351–359.
Sulikowska-Drozd A & Horsak M 2007 Woodland mollusc communities along environmental gradients in the East Carpathians. *Biologia Bratislava* **62**: 201–209.
Terhivuo J 1978 Growth, reproduction and hibernation of *Arianta arbustorum* (L.) (Gastropoda, Helicidae) in southern Finland. *Annales Zoologici Fennici* **15**: 8–16.
Umiński T 1975 Life cycles in some Vitrinidae (Mollusca, Gastropoda) from Poland. *Annales Zoologici* **33**: 17–33.