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Growth, reproduction and hibernation of Arianta arbustorum (L.) (Gastropoda, Helicidae) in southern Finland

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Field observations and experiments were made to study the growth, reproduction and hibernation of *Arianta arbustorum* in southern Finland where the species lives at the periphery of its range.

The newly hatched young become adult during their third or fourth summer. The rate of growth of the shell decreases gradually with age. The snails lay eggs from spring till autumn, most frequently in spring and early summer. The eggs hatch in 2—3 weeks. Hibernation begins earlier among adults than among subadults and juveniles, as indicated by the number of epiphragms secreted. Adults secreted more epiphragms than subadults, and subadults more than juveniles. Most specimens hibernated with the apex down. The possible adaptive value of this position is discussed. Winter mortality was greater among juveniles than among subadults, and least among adults. Totally, it was 13.6 % in 1967—1968, but only 3.4 % in 1973—1974.

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1. Introduction

Most records of *Arianta arbustorum* from Finland are confined to the coast of the Baltic up to lat. 66° N, but its Scandinavian range extends as far as Kilpisjärvi, Finnish Lapland (767:25, Grid 27° E). This species prefers habitats with a dense, rich vegetation and available calcium. Occasional population explosions have been recorded (NORDENSKIÖLD & NYLANDER 1856, NYLANDER 1858—1859, LUTHER 1901, MELA 1902, CAJANDER 1935, SUOMALAINEN 1937, E. VALOVIRTA 1955, VAPPULA 1962, I. VALOVIRTA 1964, 1967 and KAUPPI *et al.* 1968). In central and southern Europe it is eurytopic and occurs on mountain slopes up to 3000 m (LIKHAREV & RAMMEL'MEIR 1952, EHRMANN 1956, JAECKEL 1962). The life history of the species in continental Europe was described by KÜNKEL (1916) and FRÖMMING (1954) and in England by CAMERON (1969a, 1969b, 1970a, 1970b,), CAIN *et al.* (1969) and CAMERON & PALLES-CLARK (1971).

This study aims at describing the poorly known life history of *Arianta arbustorum* in southern Finland, where it lives near the periphery of its range.

2. Study area

The study area is Pappilanmäki, a hill in the oldest part of Porvoo (669:42), about 38 m above sea level. The area has been inhabited since the Stone Age and permanently since the 14th century (LUHO 1947); according to SAARISALO-TAUBERT (1963), settlement has favoured the development of a rich vegetation with many anthropochorous species. The small abandoned fields and gardens with their mould soil and heaps of fallen leaves offer good sites for hibernation.

In Pappilanmäki there is a dense population of *Arianta arbustorum* (I. VALOVIRTA 1964) which occasionally damage garden plants and pollute wells.

3. Material and methods

Snails were collected from the western slope of Pappilanmäki from an area of about 1 ha in October 1967—March 1968 and on 26 April 1974. Additional field observations were made on 13 October 1968 and on 7 May 1975. Most of the snails were preserved in 80 % alcohol, but some were used for rearing experiments conducted in Helsinki.

Experiment 1. A few adult and subadult snails hibernating in heaps of fallen leaves under snow were collected on 9 March 1968 and put into a white plastic cage (10 × 20 × 10 cm) lined at the bottom with damp blotting-paper to supply moisture, and covered with nylon net. The box was kept indoors in natural light at about + 20°C. The snails were fed with fresh cucumber and lettuce. For egg-laying there was a small box filled with garden mould. To neutralize the faeces and to prevent lack of lime, powdered chalk was sprinkled occasionally in small amounts. The eggs laid were removed daily. The culture was kept until 1 June 1968.

Experiment 2. Hibernating adults collected on 26 April 1974 and marked with instantly drying ink were put into two rearing cages (25 × 15 × 8 cm), eight specimens into each. One cage was kept outdoors protected only from direct sunshine and rain, the other in a laboratory room at about +20 °C and in natural daylight. The reproductive behaviour of the individuals was observed and the eggs laid were counted. Both groups were fed with lettuce and cucumber; some powdered chalk was added. The experiment lasted till 10 November 1974.

Experiment 3. A few newly hatched juveniles were kept in two rearing cages on 21 June to 10 November 1974. The snails in these cages were kept in the same way as those in experiment 2.

Experiment 4. Subadults and juveniles collected on 26 April 1974 were put into four cages (seven specimens in each) and treated as in experiment 2. The experiment lasted to 10 November 1974.

Arousal experiment. Snails hibernating under snow were collected in March 1968. Six groups of 18 snails of different sizes were put into glass jars with foam plastic at the bottom, with small depressions to hold the snails with the apex down. When carefully handled with forceps at —2 °C, none of the snails showed any activity. Three of the jars were kept in the dark, the other three under natural diffuse daylight in daytime and artificial light (60 W bulb about 1 m above the jars) at night. Into one jar of each group water was poured to make the foam plastic float without letting the specimens get wet. In the second jar of each group a drop of water was placed on the uppermost epiphragm of each individual, and in the third jar no moisture was added. The jars were closed tightly. The temperature was then raised from —2 to +22 °C during 12 h, and kept at this level. During each 12-h period the jars were examined 2—5 times and all the snails that had wakened were removed and measured.

The meteorological data relating to the field observations were obtained from Linnanmäki pumping station about 400 m from the study area.

Table 1. Successive size groups of *Arianta arbustorum* used in the present paper.

Age groups	Width of shell (or egg), mm $\bar{x} \pm s_{\bar{x}}$	n	Weight mg $\bar{x} \pm s_{\bar{x}}$	n
Eggs (one day old)	2.5 ± 0.02	40	11.2 ± 0.17	15
Juveniles (newly hatched)	2.7 ± 0.03	35	5.9 ± 0.24	16
range	2.2 – 3.0			
Juv. and subad. mostly	< 19.0, (up to 20.0)	–	–	–
Adults	20.1 ± 0.06,	291	–	–
range	17.4 – 24.3			

Width of shell mm	Correlation between width (×) and height (y) of shell regression line	r	n
<8	y = 0.63 × +0.124	0.979***	112
8 – <13	y = 0.74 × −0.322	0.915***	165
≥ 13	y = 0.92 × −2.072	0.870***	225
Adults	y = 0.65 × +3.011	0.577***	291

4. Results

A. Growth

The specimens were divided into size groups on the basis of shell width, but there was some overlap between adults and subadults. The adults could be recognized by the thickened outer lip framing the aperture of the shell. Individuals with a shell ≥ 15 mm wide were classified as subadults. Table 1 shows data on the different size groups of *Arianta arbustorum* distinguished in the present paper. The correlation between the width and the height of the shell is statistically significant in all these groups.

STEENBERG (1911) suggested that more or less pigmented streaks on the surface of the shell indicate where growth has ceased. In *Arianta arbustorum* most streaks are rather wide and easy to detect. No doubt, these indicate cessation of growth prior to the hibernation of the snail. Many individuals had additional streaks which were very narrow and not so easy to detect. These may indicate incidental cessations of growth caused, for example, by summer drought. Fig. 1 shows the actual width (B) of the shell of each individual on 15 October 1967 as well as the width (A) indicated by the first wide streak counted backwards from the lip of the shell in a sample of 1133 specimens. The frequency distributions show at least two peaks (4.0 and 8.5 mm in Fig. 1A, 10.5 and 14.5 mm in Fig. 1B). Fig. 2, based on the two sets of measurements in the same individuals, indicates the mean annual growth of shells of different widths. From the regression lines it can be concluded that the two peaks in Fig. 1A (and

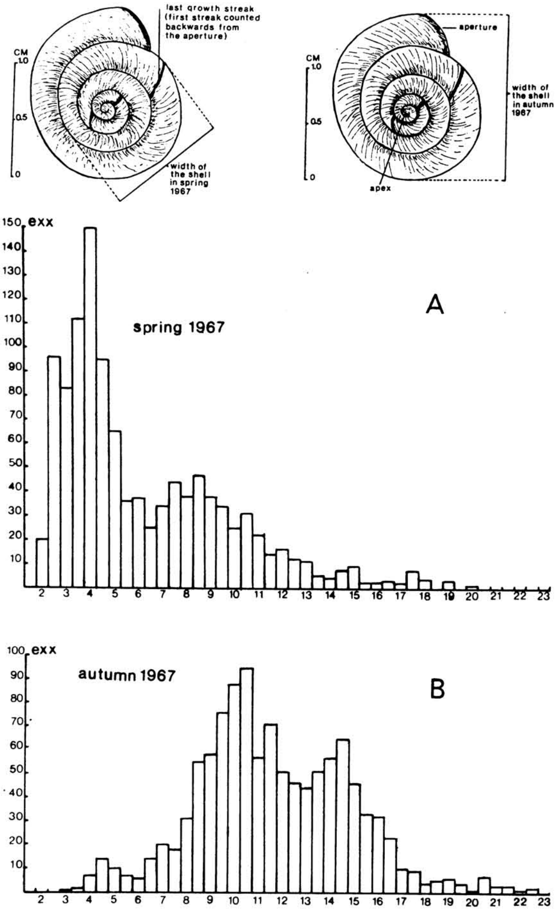

Fig. 1. The frequency distribution of shell widths (mm) in a sample of *Arianta arbustorum* collected on 15 October 1967. A = measured at the first wide growth streak situated backwards from the lip of the shell (measured as above left), B = based on the actual shell widths (measured as above right) of the same individuals as in A (n = 1133). See also the text.

B) represent snails hatched in different years. Ideally, if all the snails in each size class in spring 1967 had grown equally, the frequencies should have been the same in Figs. 1A and 1B.

Both regression lines show that the growth rate tends to decrease for shells over 11—12 mm in width. The two lines deviate because specimens of the same size group did not grow at equal rates. Hence, the best estimate for each size group lies between the lines, as also seen in Fig. 3. For the snails with a shell $\leq$ 11 mm wide the picture is blurred by the new juveniles hatched during the growth period, as indicated by field observations and the low peak (4.5 mm) in Fig. 1B. That tends to decrease the value for the mean growth of each size group and hence there are positive slopes in Fig. 2. The wider the shells of these juveniles in autumn 1967, the greater had been their annual growth, and evidently those hatched in spring 1967 had grown most, viz. 6—7 mm (black dots). Accordingly, to estimate the actual mean growth of the juveniles (2.5 mm) hatched in spring 1967 we have to extrapolate the negative slope of the regression line (open circles) upwards.

According to Fig. 2 (open circles), juveniles hatched in spring will be about 10 mm the first autumn, 14—15 mm the second, and 17—18 mm the third, becoming adult during the fourth summer of life. Some individuals may also become adult at the end of their third summer (see Fig. 3).

The sample used for the frequency distribution in Fig. 1 included 29 adults. The last annual growth of the shell among them was 3.3 mm on an average. This corresponds quite well to the values for the adults in Fig. 3.

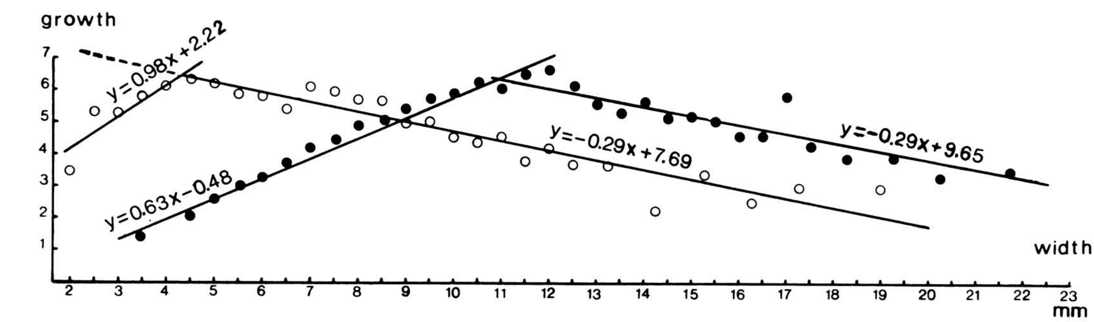

Fig. 2. Mean annual growth (mm) in the width of the shell in *A. arbustorum*. Open circles: growth among size groups of spring 1967 (based on Fig. 1A), solid circles: growth among those of autumn 1967 (Fig. 1B.) For further explanation see the text.

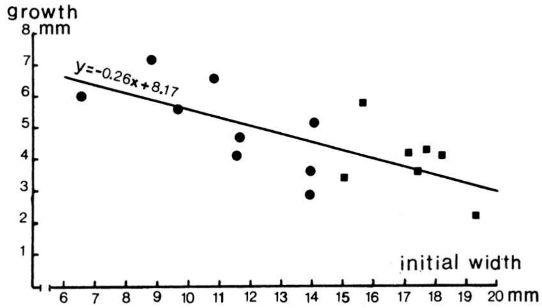

Fig. 3. Shell growth among 16 captive *Arianta arbustorum* subadults and juveniles from 26 April to 10 November 1974. Solid squares: individuals which became adults. For further explanation see the text.

To verify these results, 16 specimens were reared from 26 April to 10 November 1974 (Experiment 4). The growth of these specimens is seen in Fig. 3, where the regression line is almost the same as in Fig. 2 (open circles). Moreover, all specimens with shells ≥ 15 mm in April 1974 became adults.

The average annual growth of the shell in the newly hatched juveniles was estimated in experiment 3. For those kept outdoors it was $\bar{x} \pm s_{\bar{x}} = 4.2 \pm 0.78$ mm ($n = 8$) and for those kept indoors 6.0 ± 0.62 mm ($n = 20$). The difference is not significant ($t = 1.632$, d.f. 26).

Among the adults there was no further increase in either the width or the height of the shell (Experiment 2), as also observed by Künkel (1916).

B. Reproduction

Data on reproduction were obtained from experiments 1 and 2 and from field observations. A few clutches of eggs were found both in October 1967 and in April 1968. The latter had passed the winter but did not hatch. A few juveniles with a shell 2.5—4.0 mm wide were found in April 1974. No doubt, they had hatched late the previous autumn (see also Fig. 1B).

In experiment 2 the first mating was observed among the adults reared outdoors in May, and the first eggs were laid on 24 May 1974. In both groups the last clutches of eggs were laid in September. One mating pair was found in the study area on 7 May 1975, too. Thus egg-laying may take place from spring till autumn.

The number of eggs per clutch of reared adults was 60.2 ± 5.55 ($n = 18$, range 26—111), the confidence limits for $\bar{x}$ $_{(P = 0.95)}$ being 48.4 — 72.0. Some snails, especially those kept indoors, mated and laid eggs more than once during the experiments. One individual laid eggs three times within a period of 8 days. Both mating and egg-laying could occur at different times of day. The interval from copulation to egg-laying was less than one week, usually only a few days. Hatching took 2—3 weeks, the time being shorter indoors than out.

C. Hibernation

Onset of hibernation. Hibernation is here used to mean the physiological state in which the snail passes the winter. To follow the course of hibernation the snail population was sampled four times in winter 1967—68 (Table 2). A

Table 2. Onset and cessation of hibernation of *Arianta arbustorum* as shown by their position and the number of epiphragms secreted. Porvoo, Pappilanmäki 26 November 1967 (sample 1), 16 December 1967 (2), 9 March 1968 (3) and 30 March 1968 (4; the specimens still hibernating). The immature specimens were divided into size groups on the basis of shell width.

Sample 1	Number of epiphragms						Specimens with ≥
	0	1	2	3	4	n	3 epiphragms
Adults							
Apex down	—	—	10	8	2	20	10
Apex horizontally	—	1	3	4	—	8	4
Apex up	—	—	—	1	—	1	1
Total							(51.7 %)
Subadults and juveniles							
Apex down	1	4	22	9	—	36	9
Apex horizontally	1	5	8	1	—	15	1
Apex up	—	—	5	1	—	6	1
Total							(19.3 %)
Sample 2							
Adults	—	—	2	8	—	10	8
Subadults (≥ 15 mm)	—	—	3	6	—	9	6
Juveniles (< 15 mm)	—	1	15	13	—	29	13
Sample 3							
Adults	—	—	1	11	1	13	12
Subadults (≥ 15 mm)	—	—	27	54	1	82	55
Juveniles (< 15 mm)	—	—	39	25	—	64	25
Sample 4							
Subadults (≥ 15 mm)	—	—	4	11	—	15	11
Juveniles (< 15 mm)	—	1	28	18	1	48	19

fifth sample was taken on 26 April 1974 (Table 3). Fig. 4 gives data on temperature and snow cover.

In October 1967 no snails were yet observed to enter hibernation, but on 26 November 1967 the only snails found without epiphragms were two juveniles (Table 2), neither of them any longer active. Comparison of samples 2 and 3 shows that no epiphragms were secreted after 16 December 1967. On combining these two samples and comparing the results with those of sample 1, we see that the final number of epiphragms was secreted between 26 November and 16 December 1967 (adults $\chi^2_{\text{Yates}} = 5.29^*$ d.f. 1, subad. and juv. $\chi^2 = 20.89^{***}$, d.f. 1), evidently not after 4 December, when the daily temperature maximum was below $\pm$ 0 °C (see Fig. 4).

Table 2 (sample 1) shows that the apex-down position was preferred both by adults and by subadults and juveniles. About 60—70 % of the snails of all sizes hibernated with apex down, 25—30 % with apex horizontally and less than 15 % with apex up. Samples 2 and 3 in Table 2, taken together, show that the final number of epiphragms secreted was greater among adults than among subadults ($P_t < 0.06$), and least among juveniles ($P_t < 0.001$).

Arousal from hibernation. On 30 March 1968, of the 23 subadults found 8 (34.8 %) had no epiphragms and of the 64 juveniles 16 (25.0 %) had wakened, too. These two groups do not deviate from each other ($\chi^2 = 0.81$, d.f. 1) (Table 2, sample 4). Unfortunately, on 30 March 1968 only two adults were found, both dead and with 3 epiphragms.

The arousal of different stages from hibernation was then studied experimentally. When brought into the laboratory the snails that were alive became active within 9 days. During the first 5 days the proportion of individuals

Table 3. The arousal of *Arianta arbustorum* from hibernation at Porvoo, Pappilanmäki, by 26 April 1974. See the text.

Position and width of shell	Aroused before 26 April 1974						Not aroused by 26 April 1974					Total	
	Epiphragms						Epiphragms						
	0	1	2	3	n	%	2	3	4	n	%	n	%
Apex down													
< 8 mm	6	1	–	–	7		–	–	–	–		7	
8 – < 13 mm	15	6	–	–	21	43	–•	–	–	–	50.0	21	43
≧ 13 mm	13	5	1	–	19		1	2	–	3		22	
Adults	19	2	3	1	25	45	6	29	10	45	75.0	70	60
n	53	14	4	1	72		7	31	10	48		120	52
%					60					40			
Apex horizontally													
< 8 mm	4	2	–	–	6		–	–	–	–		6	
8 – < 13 mm	7	9	–	–	16	47	–	–	–	–	50.0	16	47
≧ 13 mm	22	8	–	–	30		–	3	–	3		33	
Adults	17	2	2	1	22	39	1	7	1	9	15.0	31	27
n	50	21	2	1	74		1	10	1	12		86	37
%					86					14			
Apex up													
< 8 mm	–	1	–	–	1		–	–	–	–		1	
8 – < 13 mm	2	2	–	–	4	10	–	–	–	–	–	4	9
≥ 13 mm	2	4	–	–	6		–	–	–	–		6	
Adults	6	1	1	1	9	16	1	5	–	6	10.0	15	13
n	10	8	1	1	20		1	5	–	6		26	
%					77					23			11
Total n	113	43	7	3	166		9	46	11	66		232	
%					72					28			

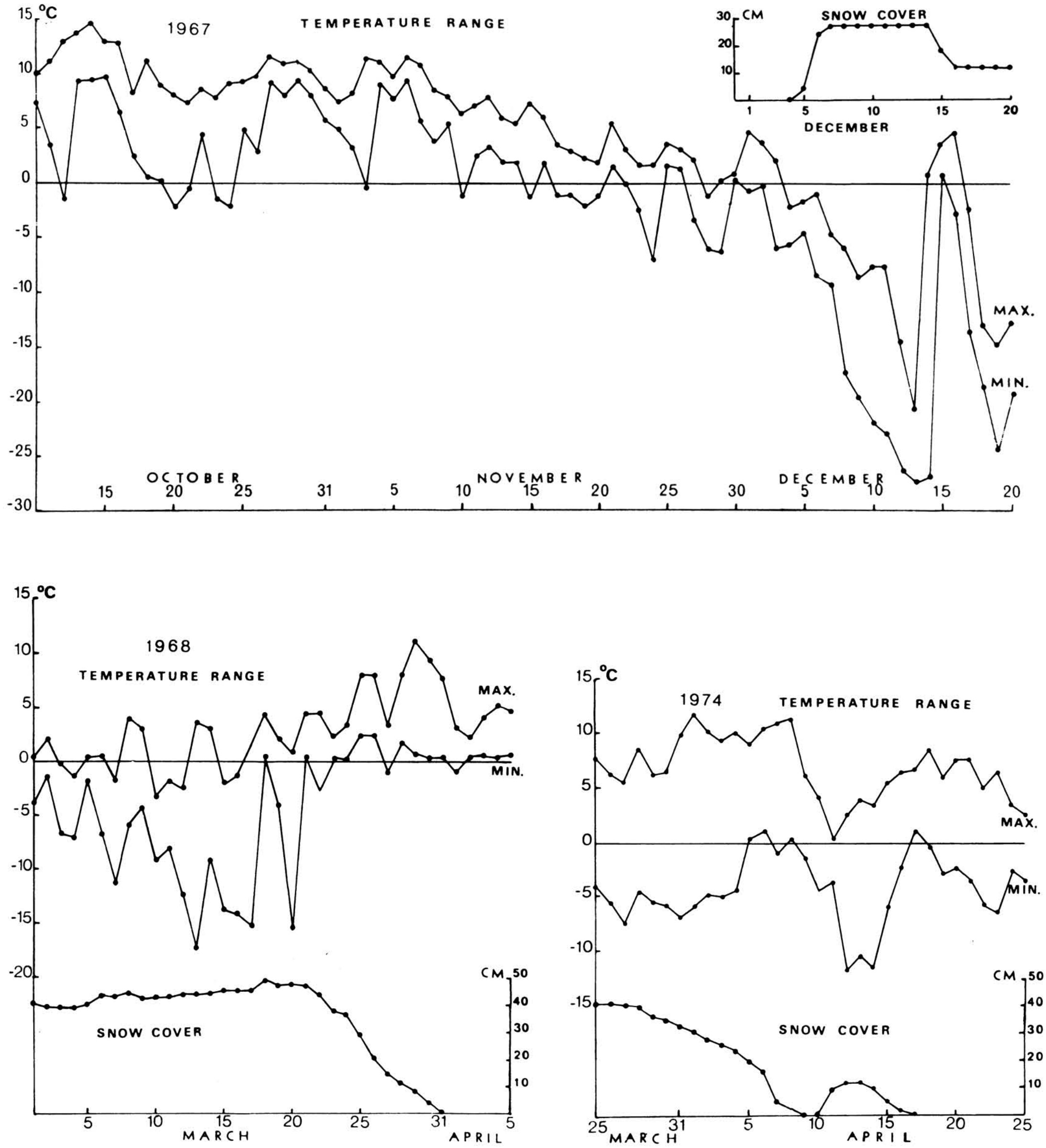

Fig. 4. Temperature range and snow cover in Porvoo, Linnanmäki, in autumn 1967, spring 1968 and spring 1974. For further explanation see the text.

activated was higher among those with a shell < 15 mm wide than among those with ≥ 15 mm. The deviation between these two groups, counted over the whole 9-day period, was significant ($P < 0.001$). In this experiment no effect of light or moisture could be detected.

If samples 2 and 3 (Table 2) are combined, the ratio of subadults with ≤ 2 epiphragms to those with ≥ 3 is 30/61 and in sample 4 it is 4/11 ($\chi^2 = 0.23$, d.f. 1), the corresponding ratios among the juveniles being 55/38 and 29/19 ($\chi^2 = 0.02$, d.f. 1). We may conclude that the wakened subadults and juveniles had the same number of epiphragms as those that were still hibernating. Thus, time of arousal does not seem to depend on the number of epiphragms (see also Table 3).

By 26 April 1974 (Table 3) 71.6 % of the specimens had wakened. About 3 weeks earlier there had been a sudden decrease in temperature and a fall of snow (Fig. 4). Presumably the specimens with no epiphragms had wakened after 17 April, when there was no snow; the others, which, when found, had newly secreted, thin, transparent epiphragms, had wakened before 10 April.

On 26 April 1974 40 % of the snails found in the apex-down position were not yet aroused. In the other two groups the corresponding figures were significantly lower, viz. 14.0 % (apex horizontally) ($P < 0.001$) and 23.1 % (apex up) ($P < 0.001$). Moreover, of all the adults 60.4 % were lying apex down, 26.7 % apex horizontally and 12.9 % apex up. Among subadults and juveniles the corresponding figures were 43.1 %, 47.4 % and 9.5 %. All the snails with shells < 13 mm wide had already wakened. If the adults that had already wakened had hibernated in the positions in which they were found, it would seem that those lying apex down hibernate longer than the others ($\chi^2 = 24.48^{***}$, d.f. 2). The individuals hibernating longer than the others in spring may have better chances of surviving spells of adverse weather.

Mortality after winter. Tables 2 and 3 refer only to snails that were alive. On 9 March 1968 13.6 % of the specimens examined were dead. On 30 March 1968 the corresponding figure was 11.2 %, showing no significant difference between the groups ($\chi^2 = 0.34$, d.f. 1). In April 1974 it was only 3.3 %. If we combine these samples, the overall winter mortality was 3.3 % among the adults, 6.7 % among the subadults and 13.5 % among the juveniles, indicating significant differences between the groups ($\chi^2 = 12.23^{**}$, d.f. 2).

4. Discussion

The method used to study the growth of the shell does not reveal whether an individual was hatched in spring or summer 1967 or in late summer or autumn 1967 (Fig. 1). Accordingly, the values in Fig. 2 (positive slopes) are somewhat too low for the former and too high for the latter group.

It was concluded that in autumn 1967 the non-reproductive part of the snail population consisted of individuals hatched in 1967, 1966, 1965, and a few possibly in 1964. Differences in the growth rate and birth date of the individuals born in the same year are due to overlapping of the age classes.

In Germany, according to KÜNKEL (1916), the growth of the shell of *Arianta arbustorum* may be completed in one year under favourable conditions, but in nature it will take two years. In France the newly hatched juveniles will become adults during their next summer (GERMAIN 1930). The same is true in the Netherlands, where the whole life span of a specimen takes 3—4 years (VAN BENTHEM JUTTING 1933). In Denmark the juveniles become adults in 15—16 months (STEENBERG 1911), but BURESCH (1911) gives newly hatched juveniles only one year to live. It is also known that the growth rate of juveniles from the same clutch may vary greatly (VAN BENTHEM JUTTING 1933). In Finland the adults hibernate at least once, and usually more than once. Before they mature they have lived 3—4 years as juveniles and subadults. Undoubtedly, the reason why their life span is considerably longer here than in Central Europe is because in Finland their period of activity is only 6—7 months.

Arianta arbustorum is usually regarded as a strict herbivore, but on 15 October 1967 I observed a few specimens eating a dying earthworm. In rearing experiments soft parts of dead snails were eaten. Moreover, some individuals were seen to eat one or two of their own epiphragms after wakening.

Many terrestrial gastropods show a tendency to aggregate (EVANS 1972:111). This is also true of *Arianta arbustorum*, but the tendency seems to vary with the season and with the age of the snail. Accordingly, the frequency distributions of Fig. 1 do not necessarily correspond to those of the actual snail population. In Fig. 1B among the juveniles hatched in 1967 (shell ≤ 12 mm) there are two frequency peaks, viz. 4.5 mm and 10—10.5 mm. This suggests two groups hatched from eggs laid in spring and in late summer, and interrupted by summer drought.

The number of eggs per clutch is given by most authors as 30—50 (60) (MOQUIN-TANDON 1855, STEENBERG 1911, GERMAIN 1930), but also as 30—90 (KÜNKEL 1911), 30—80 (TAYLOR 1882) and 60—80 (BURESCH 1911). At least the exact figures by FRÖMMING (1954:303) (40.6 ± 4.51, n = 19, range 11—65) are significantly lower than those found in experiments 1 and 2 (t = 2.755**, d.f. 35).

In Germany, specimens may lay eggs 3—4 times during their first reproduction period (KÜNKEL 1916). In experiment 2 some adults laid eggs 2—3 times. In *Cepaea nemoralis* the frequency of oviposition increases if the snails are frequently exposed to short periods of drought, but this does not affect the mean clutch size (WOLDA 1965).

In Finland *Arianta arbustorum* hibernates for 5—6 months each year and most specimens do so in the apex-down position. CARNEY (1966) observed that specimens of *Allogona ptychophora* hibernating with their aperture facing down suffered a higher winter mortality than the others. The mortality figures for the snails collected on 26 April 1974 were 2.4 % (apex down), 4.2 % (apex horizontally) and 3.6 % (apex up). Moreover, as shown in Table 3, the adults lying apex down hibernated longer than the others. This indicates a possible adaptive value of the "apex-down" position.

In general, juveniles are more frequently active than adult snails (MACHIN 1975:155). The differences between these two groups, both in the onset of hibernation and in arousal from it, may be explained by differences in their metabolism.

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References

VAN BENTHEM JUTTING, W. S. S. 1933: Mollusca (I) A. Gastropoda, Prosobranchia et Pulmonata. Fauna van Nederland 7:1—387.

BOYCOTT, A. E. 1934: Habitats of land mollusca in Britain. — J. Ecol. 22:1—35.

BURESCH, J. 1911: Untersuchungen über die Zwitterdrüse der Pulmonaten. I. Die Differenzierung der Keimzellen bei Helix arbustorum. — Diss. Leipzig.

CAIN, A. J., CAMERON, R. A. D. & PARKIN, D. T. 1969: Ecology and variation of some Helicid snails in northern Scotland. — Proc. Malacol. Soc. London 38:269—299.

CAJANDER, O. 1953: Arianta arbustorum (L.) in Tervola gefunden. — Ann. Zool. Soc. Zool.-Bot. Fennicae Vanamo 1 (5):3.

CAMERON, R. A. D. 1969a: The distribution and variation of three species of landsnail near Rickmansworth, Hertfordshire. — Zool. J. Linn. Soc. 48:83—111.

—»— 1969b: Predation by song thrushes Turdus ericetorum (Turton) on the snails Cepaea hortensis (Müll.) and Arianta arbustorum (L.) near Rickmansworth. — J. Animal Ecol. 38: 547—553.

—»— 1970a: The survival, weight-loss and behaviour of three species of land snail in conditions of low humidity. — J. Zool. (London) 160:143—157.

—»— 1970b: The effect of temperature on the activity of three species of Helicid snail (Mollusca: Gastropoda).—J. Zool. (London) 162:303—315.

CAMERON, R. A. D. & PALLES-CLARK, M. A. 1971: Arianta arbustorum (L.) on chalk downs in southern England. — Proc. Malacol. Soc. London 39:311—318.

CARNEY, W. P. 1966: Mortality and apertural orientation in Allogona ptychophora during winter hibernation in Montana. — Nautilus 79:134—136.

EHRMANN, P. 1956: Mollusca. — Die Tierwelt Mitteleuropas II (1):1—264.

EVANS, J. G. 1972: Land snails in Archaeology. — 436 pp. London.

FRÖMMING, E. 1954: Biologie der mitteleuropäischen Landgastropoden. — 404 pp. Berlin.

GERMAIN, L. 1930: Mollusques terrestres et fluviatiles I. — Faune de France 21:1—477.

JAECKEL, S. G. A. 1962: Ergängzungen und Berichtigungen zum rezenten und quartären Vorkommen der mitteleuropäischen Mollusken. — Tierwelt Mitteleuropas 2 (1) (Ergängzungen): 25—294.

KAUPPI, M., KERÄNEN, P. & HAAHTELA, I. 1968: Helicigona (Arianta) arbustorum (L.) maakotilon massaesiintymä Ulkokrunnin saarella (PP). — Luonnon Tutkija 72:94—95.

KÜNKEL, K. 1916: Zur Biologie der Lungenschnecken. — 440 pp. Heidelberg.

LIKHAREV, I. M. & RAMMEL'MEIR, E. S. 1952: Terrestrial Mollusks of the Fauna of the U.S.S.R. — Keys to the Fauna of the U.S.S.R. 43:1—574. (English transl. Jerusalem 1962)

LUHO, V. 1947: Suomen kivikauden pääpiirteet. — 174 pp. Helsinki.

LUTHER, A. 1901: Verzeichnis der Land- und Süsswassermollusken der Umgebungen Revals. — Acta Soc. Fauna Flora Fennica 20 (2):1—125.

MACHIN, J. 1975: Water relationships. — In: FRETTER, V. & PEAKE, J. (eds.): Pulmonates. Functional Anatomy and Physiology. — 417 pp. London.

MELA, A. J. 1902: Nilviäisemme. — Luonnon Ystävä 6:163—185.

MOQUIN-TANDON, H. 1855: Histoire naturelle de Mollusques terrestres et fluviatiles de France I. — 416 pp. Paris.

NORDENSKIÖLD, A. E. & NYLANDER, A. E. 1856: Finlands mollusker. — 115 pp. Helsingfors.

NYLANDER, A. E. 1858—59: Bidrag till Finlands malakozoologi. — Notiser Sällsk. Fauna Flora Fennica 4 (N.S. 1):1—126.

SAARISALO-TAUBERT, A. 1963: Die Flora in ihrer Beziehung zur Siedlung und Siedlungsgeschichte in den südfinnischen Städten Porvoo, Loviisa und Hamina. — Ann. Bot. Soc. Zool.-Bot. Fennicae Vanamo 35 (1):1—188.

STEENBERG, C. M. 1911: Bløddyr. I. Landsnegle. — Danmarks Fauna 10:1—221.

SUOMALAINEN, H. 1939: Arianta arbustorum (L.) auf der Insel Peninsaari, mitten im finnischen Meerbusen. — Ann. Zool. Soc. Zool.-Bot. Fennicae Vanamo 6 (6):13—15.

TAYLOR, J. W. 1882: Life histories of British Helices, 1. Helix arbustorum. — J. Conchology 3:241—256.

VALOVIRTA, E. 1955: Runsaasti lehtoetanoita (Arianta arbustorum [L.]) Kristiinankaupungin tienoilla. — Mem. Soc. Fauna Flora Fennica 32:101—103.

VALOVIRTA, I. 1964: Porvoon Arianta arbustorum -esiintymä. — Luonnon Tutkija 68:127—128.

—»— 1967: List of Finnish land gastropods and their distribution. — Ann. Zool. Fennici 4:29—32.

VAPPULA, N. 1962: Suomen viljelykasvien tuhoeläinlajisto. — Ann. Agricult. Fenniae, Animalia Nocentia 5 (1) (Suppl. 1):1—275.

WOLDA, H. 1965: The effect of drought on egg production in Cepaea hortensis (L.). — Arch. Neerl. Zool. 16:387—399.

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