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LIFE CYCLE AND POPULATION DYNAMICS OF *HELICODONTA OBVOLUTA* (O. F. MÜLLER, 1774) (GASTROPODA: PULMONATA: HELICIDAE)

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ABSTRACT: Life cycle of *Helicodonta obvoluta* (O. F. Müll.) was studied in the field and in laboratory. Mating lasts 2–3 hrs and includes: meeting of the partners, recognition, courtship dance, copulation, resting phase and parting. No spermatophores were observed upon dissection of a total of 90 adult individuals which seems to indicate that *H. obvoluta* does not produce them. The egg-laying snail embeds anterior part of its body 4–6 mm deep in rotting timber. The egg-laying lasts from about a dozen hours to two days. Freshly laid eggs are white, calcified, slightly translucent and get opaque in a few days. They are slightly oval, of 2.10–2.85 mm major and 2.00–2.60 mm minor diameter. In laboratory, eggs are laid in spring (March-June) and autumn (August-November), in the field, the egg-laying periods are somewhat shorter (April-beginning of June, end of August-beginning of October). Most laboratory snails laid eggs only once in their lifetime, the maximum number of egg-laying periods was four. The percentage of hatching eggs in laboratory is ca. 59%. The number of eggs per clutch ranges from 9 to 27. The incubation period ranges from 14 to 31 days, and is shorter for spring (14–18 days) compared to autumn (19–23 days) clutches. Hatching is asynchronous, lasting from 1 to 4 days. With approaching hatching, the white colour of the egg disappears, so that the young snail is surrounded only by a translucent membrane, which gets broken as a result of its movements. Newly-hatched snails have shells of 1 whorl, devoid of periostracal hairs. No egg cannibalism was observed. Out of 174 young hatched in laboratory, 159 reached maturity. During numerous dissections of adult individuals no eggs were found in the reproductive tracts; if there is an egg-retention, it must be very short-lasting. Placing eggs in rotting timber and covering them with mucus protects them from drying-out, ensures a more favourable temperature and limits accessibility to predators. The number, relative and absolute size of eggs, number of clutches per year and per lifetime, and the life span seem to be correlated with size rather than with phylogenetic position of the species. No uniparental reproduction was observed. In laboratory the time elapsing between hatching and maturity (lip completely formed) ranged from 140 to 624 days; it varied between individuals hatched in particular years and seasons, e.g. young of the spring 1997 grew much faster (mean 354 days) than those of the spring 1999 (mean 442 days). The time required to reach full size was not correlated with the ultimate number of whorls. The growth shows three distinct phases: a quick initial phase of 3–4 months, a slow phase, and a short quick phase preceding lip formation. The monthly increment depends on the growth phase: 1.15 whorl in phases 1 and 3, 0.30 whorl in phase 2. The growth rate in the field is similar to that observed in laboratory, though with a wider scatter within growth phases and some differences between years and seasons. Depending on weather conditions, the youngest age class (1) appears from April till June or from May till July, and from the end of August till the beginning of October. Thus each season two new generations are produced: spring and autumn. The spring generation, depending on the month of hatching, may complete its growth in the same season and winter as adults, or reach stage 4 or 5 and complete their growth next spring. The autumn generation always winters as immature snails which complete their growth in late spring next year. Adult snails (c. 1 year old) dominate in all the monthly samples, while older individuals are few. In laboratory, the life span ranged from 516 to 1,187 days; thus the life span of some individuals exceeds 3 years. The estimate of life span in the field, based on marking-release-recapture, is less exact, but on the whole the oldest snails in the field lived slightly over 3 years, while life span of some was only 2 years. In laboratory and in the field, the snails reproduce in spring and autumn. In laboratory, they are active (feeding, crawling) throughout the year, but in winter resting periods of a few days at a time are observed, with the aperture covered by a thin epiphragm. In the

field, the snails enter winter torpor at the end of October/beginning of November, having penetrated rotting logs from below, and stay in rotting wood with their apertures covered with thick, calcified epiphragms. Depending on weather, they get active at the beginning or end of April. Under conditions of constant temperature and humidity (indoors) adult snails show two activity peaks: late evening and early morning, with a resting period during the day. Immature individuals are more active, with a constant high activity since afternoon till mid-morning, and most remain active during the day. In conditions of variable temperature and humidity (out-doors), the activity of all age classes depends on humidity and temperature, the immature snails, like in constant conditions, being generally more active. The mobility of *H. obvoluta* is rather high, individual snails cover the distance of 4–5 or even 7 metres during a month.

KEY WORDS: life cycle, reproduction, populations dynamics, terrestrial snails, Helicidae, *Helicodonta obvoluta*

INTRODUCTION

Information on life cycle parameters is useful for phylogenetic inferences, evolutionary and population studies, and for planning conservation strategies for endangered species. Papers on gastropod life cycles constitute only a negligible fraction of publications dealing with this taxon. Out of over 1,000 extant terrestrial gastropods of Europe, representing over 30 families, life cycles have been completely or partly studied only in 61 cases (Table 1). In most cases only single parameters are known, such as mode of copulation, appearance of eggs, their number in a clutch, number of clutches in a lifetime, mode of hatching (synchronous/asynchronous), growth rate, life span (generation time) or spermatophore structure. These are fragmentary data. For many other species life cycle was inferred from changes in the population age structure and density (field observations), while no laboratory studies have been done which would make it possible to ascertain e.g. the mode of egg-laying and hatching. Including the species dealt with here, reasonably complete life cycle data exist now for only 16 species (cf. Table 1).

Helicidae – the most speciose and wide-spread family in the European malacofauna (117 species in C and W Europe; KERNEY et al. 1983) – are among the least studied with respect to their life cycles and population dynamics. Well-studied species include on the one hand those of economic importance: *Helix pomatia*, *H. lucorum*, or *H. aspersa*, on the other – some endangered species (*H. lutescens)*, all of them members of the genus *Helix*.

Depending on the value attributed by particular authors to conchological or anatomical characters, and on whether a given author was a lumper or a splitter, *H. obvoluta* was included in the subfamily Helicodontinae within Helicidae (LOŽEK 1955, ZILCH 1959–1960, KERNEY et al. 1983, RIEDEL 1988), a monotypic family Helicodontidae within Helicoidea (SHILEYKO 1978) or Hygromioidea (SHILEYKO 1991), or else subfamily Helicodontinae within Hygromiidae, Helicoidea (NORDSIECK 1987, 1993).

Helicodonta obvoluta is endangered within most of its range (CAMERON 1972, WIKTOR & RIEDEL 1992, PAWŁOWSKA & POKRYSZKO 1998, MALTZ 2003a, b). While there exists a reasonable body of information on its ecology and distribution (SCHOLTZ 1843, REINHARDT 1874, MERKEL 1894, URBAŃSKI 1948, LOŽEK 1955, WIKTOR 1956, 1959, 1964, 1972, CAMERON 1972, KERNEY et al. 1983, RIEDEL 1988, KERNEY 1999, MALTZ 1999, 2003a, b), and descriptions of its shell and reproductive system are quite many (e. g. URBAŃSKI 1957, ZILCH 1959–1960, SHILEYKO 1978), there are no published data on the life cycle of the species.

This paper is a result of five years of laboratory and field studies aimed at a re-construction of life cycle and population dynamics of the species.

Table 1. Knowledge of life cycles of European land snails

Family	Species	Knowledge of life cycle	Source
Aciculidae	*Acicula polita* (Hartm.)	fragmentary, based on field observations	DZIĘCZKOWSKI 1972
Ellobiidae	*Carychium tridentatum* (Risso)	complete	BULMAN 1990
Cochlicopidae	*Cochlicopa lubrica* (O. F. Müll.)	fragmentary, based on field observations	UMIŃSKI & FOCHT 1979, WÄREBORN 1982
Succineidae	*Succinea sarsi* (Esmark) *Succinea putris* (L.)	fragmentary	JACKIEWICZ 1980, JACKIEWICZ & ZBORALSKA 1994

Family	Species	Knowledge of life cycle	Source
Vertiginidae	*Columella edentula* (Drap.)	fragmentary	POKRYSZKO 1987, 1990a
	Columella columella (Martens)		
	Columella aspera Waldén		
	Vertigo pusilla (O. F. Müll.)	complete	POKRYSZKO 1990b
	Vertigo substriata (Jeffreys)	fragmentary	POKRYSZKO 1990a
	Vertigo alpestris Alder		
	Vertigo ronnebyensis (Westerlund)		
Chondrinidae	*Chondrina clienta* (Westerlund)	fragmentary, based on field observations	BAUR B. & BAUR A. 1995
Pupillidae	*Lauria cylindracea* (Da Costa)	complete	HELLER et al. 1997
	Pupilla muscorum (L.)	fragmentary	POKRYSZKO 2001
Valloniidae	*Vallonia pulchella* (O. F. Müll.)	fragmentary	WHITNEY 1938
Endodontidae	*Punctum pygmaeum* (Drap.)	complete	BAUR B. 1987a, 1989,
	Discus rotundatus (O. F. Müll.)	complete	KUŹNIK-KOWALSKA 1999
	Discus perspectivus (Megerle von Mühlfeld)	complete	KUŹNIK-KOWALSKA 2001 in preparation
	Discus ruderatus (Férussac)		
Arionidae	*Arion rufus* (L.)	fragmentary, based	RIEDEL & WIKTOR 1974
	Arion ater (L.)	on field observations	
	Arion subfuscus (Drap.)		
	Arion hortensis (Férussac)		
	Arion intermedius (Normand)		
	Arion circumscriptus Johnston		
	Arion lusitanicus Mabille	complete	KOZŁOWSKI 2000, KOZŁOWSKI & SIONEK 2000, 2001
	Arion fasciatus (Nilsson)	fragmentary	JORDANES et al. 1998
	Arion silvaticus Lohmander		
Vitrinidae	*Vitrina pellucida* (O. F. Müll.)	field observations	UMIŃSKI 1975, 1970, 1983, UMIŃSKI & FOCHT 1979
	Semilimax semilimax (Férussac)		
	Semilimax kotulai (Westerlund)		
	Eucobresia diaphana (Drap.)		
	Eucobresia nivalis (Dumont et Mortillet)		
Milacidae	*Tandonia rustica* (Millet)	fragmentary, based on field observations	WIKTOR 1989
Limacidae	*Limax cinereoniger* Wolf	field observations	WIKTOR 1989
	Limax tenellus O. F. Müll		
	Lehmannia marginata (Müll.)		
	Bielzia coerulans (Bielz)	complete	SMOLEŃSKA 1936, WIKTOR 1989
Agriolimacidae	*Deroceras sturanyi* (Simroth)	complete	KOSIŃSKA 1980
	Deroceras laeve (O. F. Müll.)	field observations	WIKTOR 1989 and literature contained therein
	Deroceras agreste (L.)		
	Deroceras reticulatum (O. F. Müll.)		
	Deroceras rodnae Grossu et Lupu	fragmentary	WIKTOR 1989, REISE 1995
	Deroceras praecox Wiktor		
Boettgerillidae	*Boettgerilla pallens* Simroth	fragmentary, based on field observations	WIKTOR 1989
Euconulidae	*Euconulus fulvus* (O. F. Müll.)	fragmentary, based on field observations	UMIŃSKI & FOCHT 1979

Family	Species	Knowledge of life cycle	Source
Ferussaciidae	*Cecilioides acicula* (O. F. Müll.)	fragmentary	WÄCHTLER 1929
Clausiliidae	*Cochlodina laminata* (Montagu)	fragmentary	BULMAN 1996
	Vestia elata (Rossm.)	field observations	PIECHOCKI 1982
	Alinda biplicata (Mont.)	field observations	KURNIK-KOWALSKA 1998b
	Balea perversa (L.)	fragmentary	BAUR A. 1990, BAUR A. & BAUR B. 1992
Bradybaenidae	*Bradybaena fruticum* (O. F. Müll.)	field observations	STAIKOU et al.1990
Helicidae	*Candidula unifasciata* (Poiret)	fragmentary, based	HÄNSEL et al. 1999
	Helicella itala (L.)	on field observations	
	Theba pisana (O. F. Müll.)	complete	COWIE 1984
	Arianta arbustorum (L.)	complete	TERHIVUO 1978, BAUR B. & BAUR A. 1986, BAUR B. & RABOUD 1988, BAUR B. 1990a,b
	Cepaea nemoralis (L.)	fragmentary	WOLDA 1970, 1972
	Helix pomatia L.	complete	DZIABASZEWSKI 1975, KILIAS 1985 and literature contained therein
	Helix aperta Born	fragmentary	GIUSTI & ANDREINI 1988
	Helix lucorum L.	field observations	STAIKOU et al. 1988
	Helix aspersa O. F. Müll.	complete	HERZBERG 1965, BAILEY 1975, CHARRIER & DAGUZAN 1978, DAN & BAILEY 1982, GOMOT et al. 1986, CHUNG 1987, LIGASZEWSKI 1999, MACH-PALUSZKIEWICZ 1999
	Helix lutescens (Rossm.)	complete	KORALEWSKA-BATURA 1999

MATERIAL AND METHODS

FIELD OBSERVATIONS

Field observations on *H. obvoluta* were carried out in the nature reserve Muszkowicki Las Bukowy near Henryków (Lower Silesia, SW Poland) because only in this site the population density was sufficiently high (WIKTOR 1972, MALTZ 1999, 2003a). For detailed description of the habitat see SEMBRAT (1971) and WIKTOR (1972). The observations were carried out on the transition between the oak-hornbeam and the beech forest, in a place with several fallen tree-trunks on which *H. obvoluta* occurred in abundance (Fig.1). With respect to shell measurements the studied population did not depart from the values given by other authors (Table 2).

I visited the site each month from April till October in 1997–2000. The aim of the field observations was to ascertain the life span, growth rate and range of individual migrations, as well as seasonal changes in the population age structure and density. In order to estimate the growth rate and life span, individuals collected during at least two hours were marked each month and placed on the log from which they had been collected. Marking consisted in painting with nail-varnish a narrow stripe (each month a different colour) on the upper side of the body whorl, just next to the aperture (Fig. 2). For each re-captured individual the size of shell increment since the last marking (number of whorls) and the date of the last marking were noted, then the individual was marked and released again. When the captured/re-captured individ-

Fig. 1. Nature reserve Muszkowicki Las Bukowy. Habitat of *Helicodonta obvoluta*

Table 2. Shell measurements of *Helicodonta obvoluta*.

Source parameter	URBAŃSKI 1957	ZILCH 1959–1960	SHILEYKO 1978	KERNEY et al. 1983	KERNEY 1999	Own data
Diameter (mm)	10–11	5–14	10–14	11–15	11–14	11.25–12.95
Height (mm)	5	–	5–6	5–7	–	4.55–6.00
Number of whorls	–	–	6	5–6	–	5.75–6.75

Note! ZILCH's lower value is in all probability an error

Table 3. Field marking of *Helicodonta obvoluta* in the reserve Muszkowicki Las Bukowy. Percentage of recaptures

	n		%
Total number of snails	2547		100,00
Number of snails marked once	2075		81.47
Number of snails marked more than once:	472		18.53
marked 2×		387	15.19
marked 3×		73	2.87
marked 4×		10	0.39
marked 5×		1	0.04
marked 6×		1	0.04

Table 4. *Helicodonta obvoluta*. Age classes

Age class:	Description:
J1	Number of whorls: 1.0–2.0
J2	Number of whorls: 2.01–3.0
J3	Number of whorls: 3.01–4.0
J4	Number of whorls: 4.01–5.0
J5	Number of whorls: 5.01 – till lip formation (~6.0)
A1	Adult, aged 1 (since lip completion), periostracum undamaged, with distinct hairs
A2	Adult, aged 1+, periostracum partly or wholly damaged

ual was adult, the stripe was placed on the external or ventral side of the whorl. In the case of juvenile individuals the marking made it possible to read the shell increment since the last marking. The total number of marked and re-captured individuals is given in Table 3.

Marking aimed at ascertaining the range of individual migrations and the minimum population area was carried out in October 1997 (57 marked individuals) and September 1998 (64 individuals). It consisted in marking groups of individuals from logs other than those which served for growth and life-span observations. Each group was marked with a different colour (dot at the apex, and in the case of juveniles additionally a stripe at the aperture). The marked snails were placed on their logs of origin; upon re-capture I measured the distance between the place of finding and the place of release following marking. The time between the marking and re-capture and the distance covered by the snails made it possible to calculate the range and rate of individual migrations.

Fig. 2. *Helicodonta obvoluta*. Marked snails in the habitat

In order to estimate the age structure I adopted age classes based on the number of whorls in juvenile and the degree of damage to periostracum in adult individuals (Table 4). Based on laboratory observations on the age-related damage to periostracum it was found that in about a year from maturation the periostracum disappeared almost completely. Accordingly, two age classes were distinguished within the group of mature individuals: one year old and older.

LABORATORY CULTURE

The laboratory culture was started on October 21st, 1996 and maintained till June 30th, 2001. The snails (69 individuals) were collected in the nature reserve Muszkowicki Las Bukowy in October 1996 (21 adult and 15 juvenile) and in July 1998 (33 juvenile). During the whole period of laboratory observations I kept a total of 243 individuals, of which 69 were caught in the wild and 174 hatched from eggs laid in the laboratory. From spring 1997 till autumn 1999 I obtained 32 clutches of a total of 549 eggs from which 174 individuals hatched, and 159 of them reached maturity. Including the juveniles brought from the field, a total of 228 adults were reared in the laboratory.

Adult individuals were kept in glass terraria of 29 × 18 × 30 cm, covered with polythene foil to ensure con-

stant humidity. The bottom of the terraria was covered with tissue-paper with a layer of leaf-litter and fragments of bark and 15–20 cm pieces of dead timber brought from the site. Some of the timber pieces were placed vertically so as to create daytime shelters for the snails. Due to their porosity they provided also an adequate substratum for egg-laying. Each terrarium contained 10–15 individuals. Newly-hatched juveniles were transferred to Petri dishes, 8 cm in diameter, lined with tissue-paper and with bits of timber. With increasing size the snails were transferred to larger dishes and, when adult, placed in terraria. The air humidity in the dishes and terraria was practically constant, close to 100%, due to the presence of a plastic dish with water or a wet cube of tissue-paper. The temperature in the room ranged from 15–18°C in winter to 20–24°C in summer. The containers were aired, tissue-paper exchanged and water supplied once a week; during periods of intense observations (e.g. reproductive period) the containers were checked daily or every 2–3 days.

Preliminary tests during the first year of the studies made it possible to ascertain food preferences and preferred sources of calcium. Pieces of chalk or dolomite tablets were added as calcium source. The snails were fed with mushrooms (champignon, chanterelle, *Boletus*) or fungi developing on the logs in the site, lettuce or cabbage leaves, cucumber and carrot.

The objective of the laboratory observations was to ascertain: growth rate, longevity, ability/inability to reproduce uniparentally, fertility, mode of copulation and egg-laying, incubation period, hatching, circadian and annual activity.

To estimate the growth rate juvenile snails were marked at monthly intervals in the same way as in the field.

To facilitate observations on life span, egg-laying, readiness to copulate, diurnal activity, adult snails were marked individually with numbers glued to their shells or a combination of symbols painted with nail-varnish on the apex (Fig. 3).

To confirm or exclude the ability to reproduce uniparentally, five individuals were kept singly in glass containers of 14 × 14 × 19 cm from early juvenile stages (J2 or J3) till death.

To estimate fertility and reproductive success I observed places of egg-laying (the eggs are laid in rotting timber) and counted the eggs, assessed the duration of incubation period and the number of hatched juveniles. Individual marking made it possible to assign clutches to individuals, provided they were observed during egg-laying.

Some of the eggs were measured with calibrated eye-piece in order to estimate the size variation; such eggs however failed to develop as a result of their removal from rotting timber.

From May till October 2000, I observed the circadian activity of *H. obvoluta*. The observations involved 13 juvenile and 12 adult individuals during 24 hours (10 observation sessions). The state of activity was estimated every hour based on the following criteria: [0] – snail retracted deep into the shell, sometimes a thin epiphragm in the aperture; [1] – snail partly retracted into the shell or extended but with contracted head; [2] – snail extended, not moving, tentacles retracted or partly everted; [3] – snail moving, feeding, copulating or examining the substratum with its tentacles. The circadian activity was observed under constant and variable temperature and humidity conditions. For observations under variable conditions the containers were covered with gauze and placed outdoors in a shady place among vegetation (simulating natural conditions). Besides estimates of the activity, the air temperature and humidity were measured with room higrometer. Due to these observations I could observe three instances of mating (not observed on other occasions because mating takes place in the night).

Statistical analysis of the results was performed with Microsoft Excel 2000 (NELSON 1999), the methods were selected based on relevant literature (ŁOMNICKI 1995).

Fig. 3. *Helicodonta obvoluta*. Marked snails in the laboratory culture

RESULTS

MATING

Three instances of mating were observed in the laboratory on May 1st, August 14th and September 15th, 2000. Mating took place during the night, between 23.00 and 3.00.

Mating included six phases: meeting, recognition, courtship dance, copulation, rest and parting (Figs 4, 5). Several times I observed failed attempts at mating, including the first two phases plus initial stages of courtship dance (making one circle). Such situations took place when a new individual was introduced into a container where several other specimens had been kept for some time. Each snail of the group took part in recognising the new-arrival which could prove to be a potential partner. Individuals kept in a group of constant composition for a few months were not observed to behave in such a way.

Mating lasted from 2 to 3 hours, the longest phase being the courtship dance which could take up to 1.5 hour, and the rest following copulation (up to 40–50 minutes).

Meeting was the first phase of mating. The snails approached each other, and stopped at a short distance (Fig. 4).

Recognition consisted in examining the partner's head and sides of foot with the tentacles, mutual touching of tentacles (Fig. 4), scraping with radulae which was usually accompanied by raising the anterior part of the foot of both partners. The phase lasted 1–2 minutes.

Courtship dance. After recognition the snails moved apart, each making a circle, to meet again soon. The circles made by the partners were either mirror images, or the snails moved in opposite directions (Fig. 4). The diameter of the circle did not exceed 8–9 cm and decreased with approaching copulation. The number of circles per snail ranged from 11 to 16. During courtship the penes became partly everted (Fig. 6). In the first stage (2–3 circles) a distinct swelling was visible around the gonopore, in later stages the gonopore opened and a gradual eversion of copulatory organs took place.

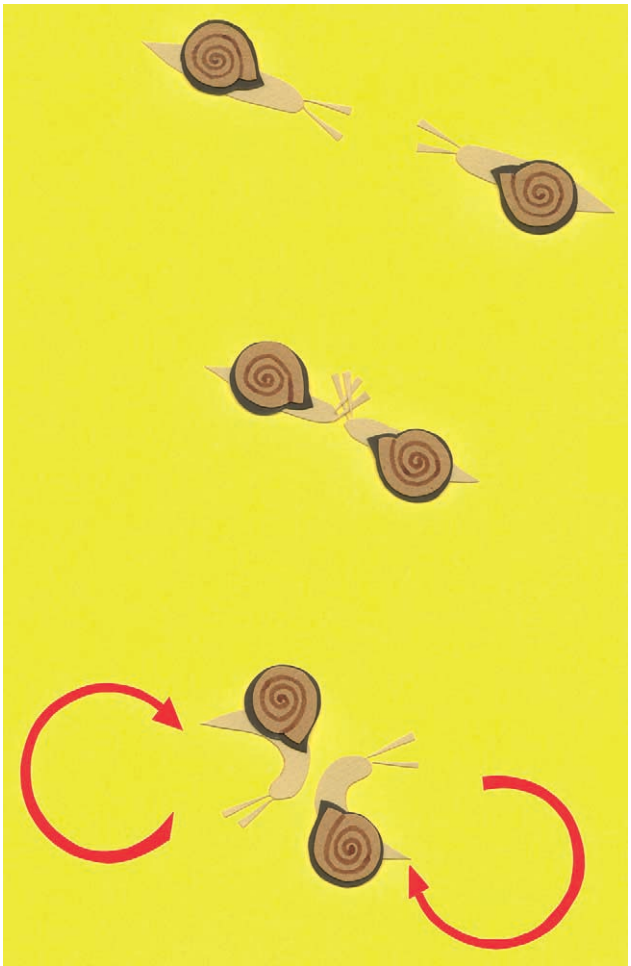

Fig. 4. Mating of *Helicodonta obvoluta*: top – meeting, centre – recognition, bottom – courtship dance

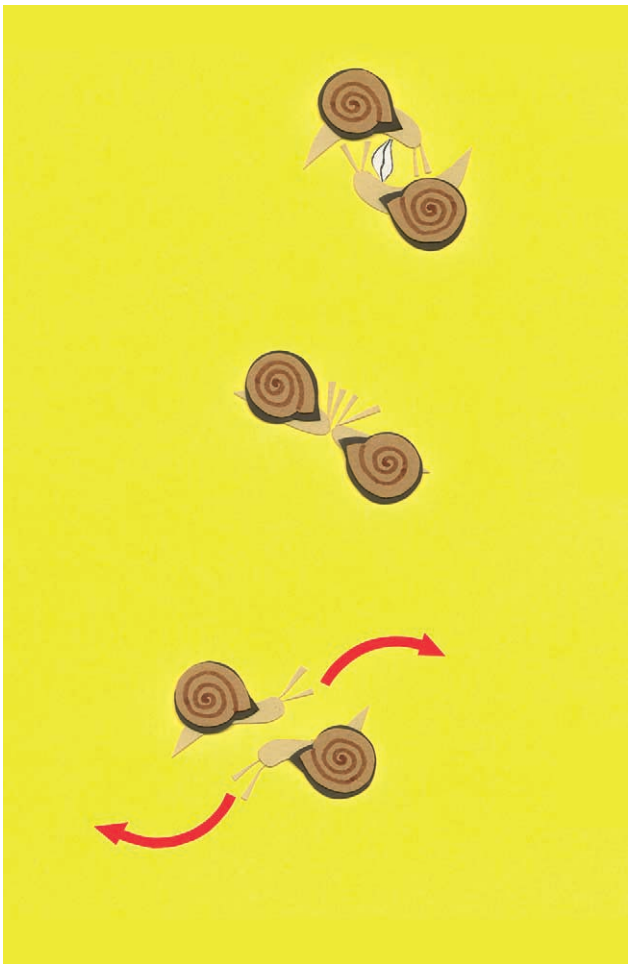

Fig. 5. Mating of *Helicodonta obvoluta*: top – copulation, centre – resting phase, bottom – parting

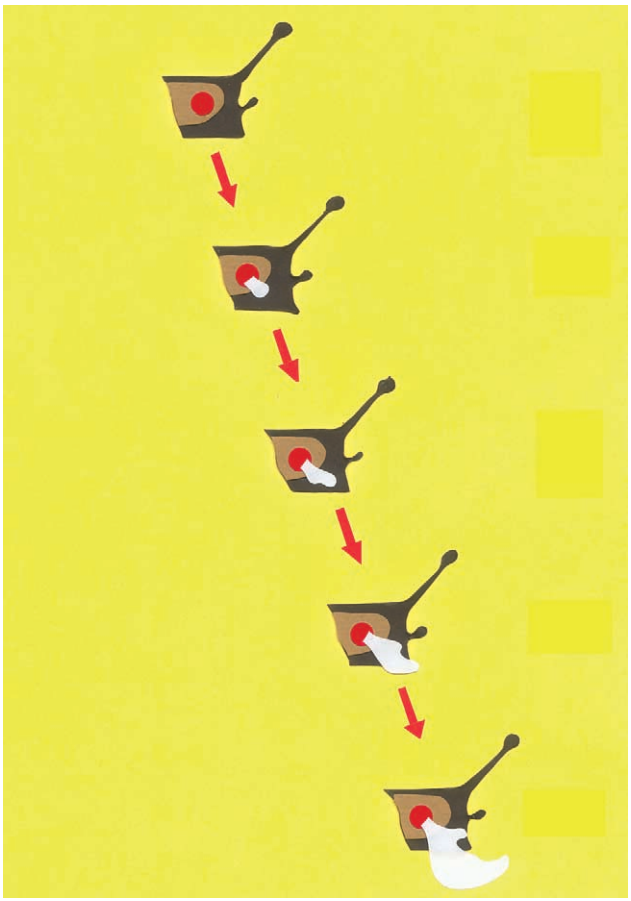

Fig. 6. *Helicodonta obvoluta*. Penis eversion

Copulation, lasting 10–12 minutes, started with a rapid eversion of entire penis by both partners which positioned themselves parallelly to each other, bodies slightly arcuately bent resulting in an elliptical configuration (Figs 5, 7). During 2–4 minutes the snails made rapid movements with their heads, each scraping the partner's penis with the radula which probably aided sperm transfer. At the same time streaks of white liquid were observed to move inside penis which was semi-transparent. During the next few minutes the partners stayed motionless, then retracted their penes, while the bodies contracted somewhat, with their anterior parts raised and tilted backwards, which lasted ca. 2 minutes.

Fig. 7. *Helicodonta obvoluta*. Copulation

Copulation was followed by resting phase. The snails, with slightly contracted tentacles, stayed motionless during up to 50 minutes, while their mouths remained in contact (Fig. 5).

Parting was the last phase of mating (Fig. 5). Following mating the snails sought shelter in shady places, e.g. under bark or in cracks in rotting timber, and remained there for a few to about a dozen hours.

I could not determine the time elapsing between mating and egg-laying, since none of the mated snails was observed during oviposition.

EGG-LAYING, INCUBATION, HATCHING

Both in the laboratory and in the field *H. obvoluta* laid eggs under bark and in cracks in rotting timber. The egg-laying snail inserted its anterior part in the crack, with retracted tentacles, to a depth 4–6 mm. The egg-laying lasted from about a dozen hours to two days.

Freshly-laid eggs were white, calcified and slightly translucent. After a few days they became completely opaque. They were slightly oval, almost spherical (Fig. 8). Their major diameter ranged from 2.10–2.85 mm (mean 2.46, SD=0.20, n=63), the minor diameter from 2.00 to 2.60 mm (mean 2.27, SD=0.18, n=63) (Table 5).

In the laboratory eggs were laid in two periods: spring (March 21st – June 28th) and autumn (August 12th – November 6th), while in the field the egg-laying took place from the end of April till the end of June and from the end of August till the beginning of October.

Thirty two clutches were laid in the laboratory from March 21st, 1997 till June 2nd, 2000. Out of 16

Fig. 8. Eggs of *Helicodonta obvoluta*: 1 – normal clutch, 2 – eggs in a common envelope

Table 5. *Helicodonta obvoluta*. Egg characters

	Major diameter (mm)	Minor diameter (mm)	Major to minor diameter ratio
Mean	2.459	2.265	1.039
Standard error	0.025	0.022	0.028
Median	2.400	2.200	1.070
Standard deviation	0.202	0.176	0.219
Variance	0.041	0.031	0.048
Minimum	2.100	2.000	0.080
Maximum	2.850	2.600	1.210
Number of measurements	63	63	63

snails which were assigned particular clutches only four were born in the laboratory, the remaining 12 were brought from the field as juveniles (4) or adults (8) (Table 6).

Out of the 32 clutches, juvenile snails hatched out of 17, which is 53.13% of all clutches (Table 7). The percentage is higher (58.62%) when the eggs which did not hatch as a result of being transferred from timber to tissue paper (3 clutches of the spring 1997, measured eggs are ommitted).

Besides the typical, single eggs, laying of atypical eggs – 3 or 4 in a common envelope – was observed twice. No juveniles hatched from these eggs (Fig. 8). They were a part of normal clutches but their position in the clutch indicated that they were the last to be laid. Within 5–7 days from laying they decomposed.

The number of eggs per clutch ranged from 9 to 27 (mean 17.16, SD=4.48, n=32). For clutches from which juveniles hatched the respective values were 9–23, 15.65, SD=4.05, n=17. The number of hatched juveniles in such clutches ranged from 2 to 19 (mean 10.24, SD=4.18, n=17), the number of resulting adults was 2–17 (mean 9.35, SD=3.81, n=17).

The incubation period ranged from 14 to 31 days (mean 21.94, SD=5.01, n=17). The incubation of autumn clutches lasted: 19–23 days (August, temperature 21–23°C) and 20–30 days (September, temperature ca. 20°C), of spring clutches 14–18 days (April and beginning of May, temperature 17–19°C) and 23–31 days (May, temperature 21–24°C).

Hatching was asynchronous, and lasted 1–4 days within a clutch (mean 3.18, SD=0.88, n=17). The symptoms of approaching hatching were: disappearance of the white colour of the egg which became translucent, so that the young snail could be seen inside, now surrounded only by a translucent membrane. The membrane was easy to break for the young snail. Newly-hatched juveniles had shells of one

Table 6. *Helicodonta obvoluta*. Egg-laying by 16 individuals in laboratory culture

No. of snail	date of hatching	date of death	life span (days)	number of clutches	Dates of egg-laying			
1	F (A) 21.10.96	24.11.98	~ 1133	2	9.04.97	19.09.98		
2	F (A) 21.10.96	14.08.98	~ 1031	1	7.05.97			
3	F (A) 21.10.96	12.12.98	~ 1148	2	21.03.97	20.08.98		
4	F (A) 21.10.96	30.09.98	~ 1078	1	22.05.97			
5	F (A) 21.10.96	10.10.98	~ 1088	2	4.04.97	23.08.98		
6	F (A) 21.10.96	22.12.97	~ 832	1	30.05.97			
7	F (A) 21.10.96	29.08.98	~ 1077	1	21.05.97			
8	F (A) 21.10.96	15.12.98	~ 1151	1	24.10.98			
9	F (J) 21.10.96	10.12.99	~ 1105	3	6.11.98	25.05.99	15.10.99	
10	19.04.97 L	15.08.00	1187	4	24.09.98	6.05.99	3.09.99	27.05.00
11	14.04.97 L	15.05.00	1125	1	12.05.99			
12	28.04.97 L	15.09.99	870	1	24.05.99			
13	28.04.97 L	15.02.00	1023	2	9.04.99	29.10.99		
14	F (J) 15.08.98	15.07.00	~ 787	1	25.05.99			
15	F (J) 15.08.98	15.12.00	~ 950	1	28.06.99			
16	F (J) 15.08.98	15.12.00	~ 962	1	12.08.99			

F – brought from the field as: A – adult (aged 1), J – juvenile (~50 – 60 days); L – hatched in laboratory

Table 7. *Helicodonta obvoluta*. Egg clutches. Incubation duration. Hatching

Reproductive season	Date of egg-laying	Number of eggs	Incubation (days)	Date of hatching	Hatching duration (days)	Number of young	Number of adults
S97/1	21 III 97	16	22	10–13 IV	4	11	11
S97/2	4 IV 97	12	14	16–19 IV	4	9	9
S97/3	9 IV 97	14	18	26–29 IV	3	7	7
S97/4	7 V 97	13	23	31 V–2 VI	3	9	9
S97/5	21 V 97	9	31	19–21 VI	3	7	7
S97/6	22 V 97	21	24	16 VI	1	2	2
S97/7	25 V 97	27	–	–	–	–	–
S97/8	30 V 97	16	–	–	–	–	–
S97/9	3 VI 97	21	–	–	–	–	–
A98/1	20 VIII 98	19	23	9–12 IX	4	12	12
A98/2	23 VIII 98	17	21	9–12 IX	4	13	13
A98/3	19 IX 98	15	27	14–16 X	3	13	13
A98/4	24 IX 98	23	20	16–19 X	4	17	17
A98/5	24 X 98	19	–	–	–	–	–
A98/6	30 X 98	23	–	–	–	–	–
A98/7	6 XI 98	12	–	–	–	–	–
S99/1	9 IV 99	18	17	24–26 IV	3	13	10
S99/2	6 V 99	14	16	20–22 V	3	12	12
S99/3	12 V 99	13	16	27–28 V	2	9	8
S99/4	24 V 99	23	25	15–18 VI	4	19	13
S99/5	25 V 99	15	27	20–21 VI	2	7	5
S99/6	28 V 99	21	–	–	–	–	–
S99/7	4 VI 99	18	–	–	–	–	–
S99/8	17 VI 99	19	–	–	–	–	–
S99/9	28 VI 99	26	–	–	–	–	–
A99/1	12 VIII 99	11	19	30 VIII–1 IX	3	8	6
A99/2	3 IX 99	13	30	30 IX–3 X	4	6	5
A99/3	8 X 99	16	–	–	–	–	–
A99/4	15 X 99	20	–	–	–	–	–
A99/5	29 X 99	17	–	–	–	–	–
S00/1	27 V 00	11	–	–	–	–	–
S00/2	2 VI 00	17	–	–	–	–	–

S – spring generation, A – autumn generation

whorl, with no periostracal hairs. Subsequent whorls, formed after hatching, were provided with such structures. Unhatched eggs did not become translucent, but turned brown and decomposed.

The juveniles remained in their birth place from 1 to 2 days, then started travelling in search of food. I have not observed egg cannibalism within or between clutches.

Out of 485 eggs (64 eggs transferred to tissue-paper after measurements ommitted) laid in the laboratory, juveniles hatched from 174, i.e. 35.88%. Out of the 174 juveniles (100%), 159 individuals reached maturity (91.38%) (Table 8).

GROWTH

Laboratory observations

The time from hatching till growth completion (lip fully formed) ranged from 140 to 624 days (mean 379, SD=90, n=159). The time varied between the reproductive seasons (spring 1997 – autumn 1999) (Table 9). The juveniles hatched in the spring 1997 grew much faster (140–442 days, mean 354) than those of spring 1999 (361–540 days, mean 442). The mean difference was 88 days and was statistically significant (two-sided t-test, p=0.000). For the autumn generations the respective time was: autumn 1998

Table 8. *Helicodonta obvoluta*. Reproductive success

Number of clutches									
Total			Unhatched			Hatched			
29	100%		12	41.38%		17	58.62%		

Number of eggs									
Total		Unhatched		In hatched clutches					
				Total		Unhatched		Hatched	
485	100%	311	64.12%	266	54.85%	92	34.59%	174	65.41%

Number of young obtained from eggs							
Number of young & total number of eggs				Number of young & number of eggs from hatched clutches			
Total eggs		Young		Eggs from hatched clutches		Young	
485	100%	174	35.88%	266	100%	174	65.41%

Number of adults obtained from eggs and juveniles											
Number of adults & number of eggs						Number of adults & number of young					
Total eggs		Adults		Eggs from hatched clutches		Adults		Young		Adults	
485	100%	159	32.78%	266	100%	159	59.77%	174	100%	159	91.38%

Table 9. *Helicodonta obvoluta*. Number of days from hatching till ultimate size (general data). Laboratory

	Spring 1997	Autumn 1998	Spring 1999	Autumn 1999	Total (spring 97–autumn 99)
Mean	354.49	312.95	442.13	534.82	379.05
Standard error	12.40	5.32	6.26	26.85	7.14
Median	384	308	452	562	383
Standard deviation	83.201	39.426	43.375	89.059	90.064
Variance	6922.48	1554.42	1881.43	7931.56	8111.54
Minimum	140	182	361	411	140
Maximum	442	380	540	624	624
Number of snails	45	55	48	11	159

from 182 to 380 days (mean 313), autumn 1999 – 411–624 days (mean 535). The mean difference (222) was also statistically significant (same test, p=0.000).

The number of days necessary to complete growth was not correlated with the number of whorls of adult individuals. Shells of both slow-growing (over 400 days) and fast-growing (less than 300 days) snails had over 6 whorls.

During growth three phases could be distinguished: initial phase, slow-down phase and terminal phase. In the initial phase (the first 3–4 months) the growth was quicker while in the later period the growth rate decreased, and only before lip formation a certain acceleration was observed (Fig. 9). Out of 164 snails whose growth was recorded, five departed from the general pattern. Three snails of the spring generation 1999, and two of the autumn generation of the same year terminated their growth without lip formation. They reached 3.88, 3.94, 4.13, 3.13, 4.50 whorls, respectively. They stayed alive till the end of the laboratory observations in the spring 2001.

The monthly whorl increment dependend on the phase of growth: in initial phase of growth (J1) it was the greatest (mean 1.15, SD=0.37, n=167), in the slow-down phase (J5) it was the smallest (mean 0.31, SD=0.20, n=348) (Table 10).

The monthly growth increment for the spring and autumn generations was similar, except for some small differences in the maximum values of increment in stages J3 of autumn 1998 and 1999 (difference 0.2 whorl) and J4 of the same seasons (0.5 whorl), or minimum values in stages J1 of spring 1997 and 1999 (0.6 whorl) and J1 of autumn 1998 and 1999 (0.2 whorl).

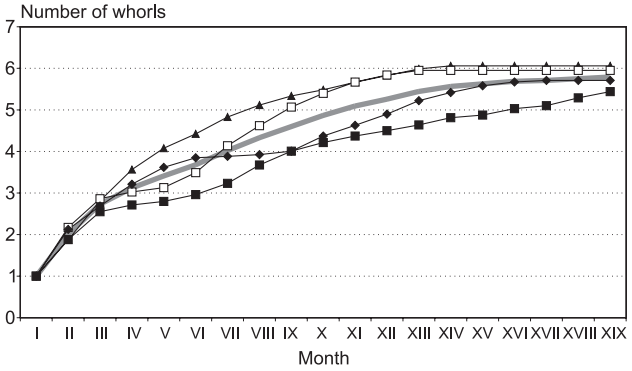

Fig. 9. *Helicodonta obvoluta*. Growth rate. Laboratory culture (1997–1999): grey line – mean of means, remaining lines – mean growth rate: triangles – spring '97, hollow squares – autumn '98, solid lozenges – spring '99, solid squares – autumn'99

Field observations

Snails at stage J1 were too small to be marked in the field, hence the observations included stages J2-J5. The whorl increment was the greatest at stage J5 (mean 0.50 whorl). Snails at stage J2 had a smaller monthly whorl increment (mean o.39), while snails at stage J3 showed the smallest increment (mean 0.35). In subsequent stages the increment increased slightly (Table 11).

The growth rate was more diverse (0.06–0.90 whorl/month, mean 0.43) in J2 snails of autumn generations compared to the corresponding stage of spring generations (0.25–0.61, mean 0.37). The monthly whorl increment in autumn J3 (0.06–0.75, mean 0.35) was similar to that observed in spring generations (0.13–0.75, mean 0.36) (Table 12).

The growth increment in particular stages varied between the years. I have observed differences in growth rate of stages J2, J3 and J4 of two years (1999 and 2000). The monthly increment was less varied in 1999 (for J2 mean 0.32, for J3 mean 0.34, for J4 mean 0.39) compared to 2000 (the respective means: 0.50, 0.20, 0.30) (Table 13).

A comparison of the laboratory and field results reveals that the monthly whorl increment decreases in consecutive growth stages in the laboratory (J2, mean 0.49, J3 0.39, J4 0.31, J5 0.31) compared to that increment observed in the field (the respective means 0.39, 0.35, 0.36, 0.53) (Tables 10, 11).

POPULATION AGE STRUCTURE

Seasonal changes in the population age structure in 1999, considering the spring and autumn generations, are presented in Figure 10.

Depending on weather conditions (temperature, rain), the smallest snails (stage J1) appeared from April till the end of June (1999) or from May till July (2000) and again from the end of August till the beginning of October (both years). As a result two generations: spring and autumn, could be distinguished each year. The spring generation, depending on the month of hatching, may terminate their growth before winter and hibernate as adults (snails hatched in

Table 10. *Helicodonta obvoluta*. Whorl increment per month (general data). Laboratory

	J1	J2	J3	J4	J5
Mean	1.153	0.496	0.399	0.314	0.306
Standard error	0.029	0.021	0.015	0.011	0.011
Median	1.130	0.500	0.380	0.250	0.250
Standard deviation	0.369	0.343	0.266	0.211	0.202
Variance	0.136	0.117	0.071	0.044	0.041
Minimum	0.130	0.000	0.000	0.000	0.000
Maximum	2.000	1.250	1.130	1.000	1.000
Number of snails	167	261	332	387	348

Table 11. *Helicodonta obvoluta*. Whorl increment per month. Field

	J2	J3	J4	J5
Mean	0.399	0.352	0.361	0.532
Standard error	0.043	0.029	0.025	0.042
Median	0.310	0.360	0.300	0.500
Standard deviation	0.215	0.196	0.211	0.309
Variance	0.460	0.039	0.044	0.096
Minimum	0.060	0.060	0.020	0.060
Maximum	0.900	0.750	1.100	1.360
Number of snails	25	45	72	55

Table 12. *Helicodonta obvoluta*. Whorl increment per month. Comparison of J2 and J3 stages from autumn and spring generations. Field

	Autumn J2	Spring J2	Autumn J3	Spring J3
Mean	0.431	0.374	0.345	0.358
Standard error	0.086	0.039	0.044	0.039
Median	0.500	0.290	0.360	0.310
Standard deviation	0.284	0.147	0.206	0.191
Variance	0.081	0.021	0.042	0.037
Minimum	0.060	0.250	0.060	0.130
Maximum	0.900	0.610	0.750	0.750
Number of snails	11	14	22	23

Table 13. *Helicodonta obvoluta*. Whorl increment per month. Comparison of two seasons (1999 and 2000). Field

Generation	Mean	Standard error	Median	Standard deviation	Variance	Minimum	Maximum	Number of snails
J2/1999	0.322	0.046	0.26	0.139	0.019	0.13	0.58	9
J3/1999	0.342	0.047	0.34	0.189	0.036	0.06	0.64	16
J4/1999	0.390	0.050	0.29	0.261	0.068	0.12	1.10	27
J5/1999	0.553	0.065	0.50	0.325	0.105	0.06	1.36	25
J2/2000	0.507	0.072	0.57	0.189	0.036	0.25	0.74	7
J3/2000	0.199	0.058	0.13	0.174	0.030	0.06	0.63	9
J4/2000	0.330	0.049	0.25	0.205	0.042	0.12	0.90	17
J5/2000	0.493	0.089	0.50	0.320	0.102	0.06	1.00	13

April) or reach stage J4-J5 and resume and complete growth next spring (snails hatched in May and June). The autumn generation always hibernates as juveniles which terminate their growth in late spring (snails hatched in August) or in autumn (snails hatched in September and October). Because of the varied growth rate, the two generations often overlap at stages J3, J4 and J5 which has a considerable effect on the number of snails obtained during collecting material of each age class. In all monthly samples adult snails clearly dominated (A1), while senile snails (A2) were few (2.9–14.4% sample) (cf. Fig. 10).

The population density fluctuations can be estimated on the basis of monthly collections (snails collected for marking purposes). The total number of individuals collected on each occasion ranged from 51 to 129, and in all cases except the 20th of October 2000 (snails already preparing to hibernate, see "annual activity") it exceeded 80. This indicates that the density fluctuations between months are rather insignificant, and result from weather conditions rather than from intense mortality in a particular season.

LIFE SPAN

Laboratory observations

The laboratory culture contained snails brought from the field as juveniles (stages J2, J3, J4) and snails born in the laboratory. In the former case it was difficult to estimate the life span, since the approximate duration of life in the field (estimate based on field data on growth rate, see below "Life span – field observations"), had to be added to the duration of life in the laboratory. For this reason the data on the life span were divided in two groups (Tables 14, 15).

The life span ranged from 516 to 1,187 days (mean 959.10, SD=119.64, n=136). The five individuals kept singly in order to test the ability to reproduce uniparentally had the shortest life span (516, 654, 694, 724 and 792 days, respectively). Out of 136 snails, the life span of 54 (39.7% studied individuals) exceeded 1,000 days (1,002–1,187). This means that the life span of some laboratory individuals exceeded 3 years.

Field observations

The estimate of life span based on field observations is very rough, since the multiple markings involved almost exclusively adult, subadult and senile snails (cf. Table 3). The senile snails had to be excluded since it was impossible to estimate their life time prior to the first marking. The estimate of the duration of life prior to the first marking was based on the mean growth rates in the field (juvenile snails) and mean rate of periostracum damage in the laboratory (adults), with the following values: age class A1 – 548 days, subadult (A1* in Table 15) – 365 days, juvenile (J5) – 210 days.

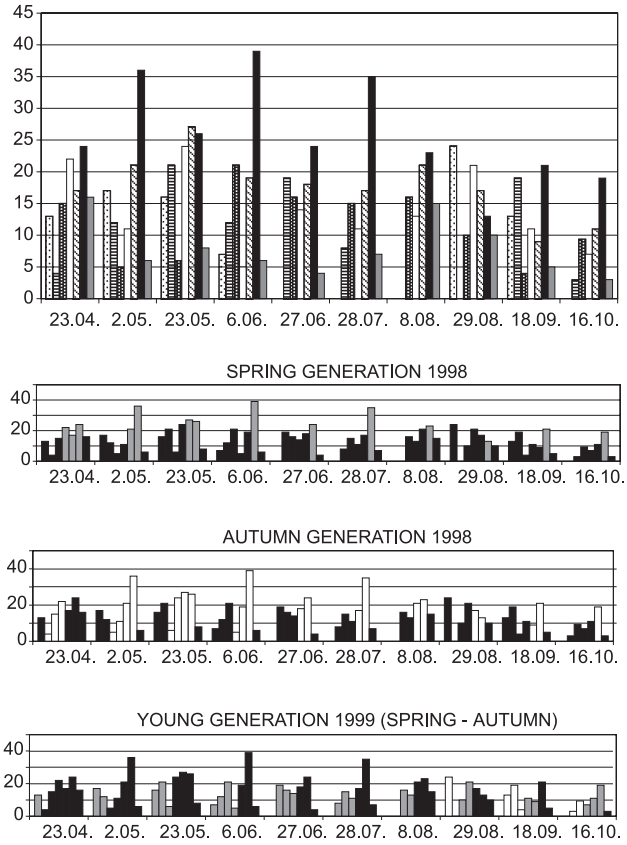

Fig. 10. Age structure of the population of *Helicodonta obvoluta*. Muszkowice 1999. Top graph: Black dots on white – J1, horizontal hatching – J2, white dots on black – J3, white – J4, oblique hatching – J5, black – A1, grey – A2; centre and bottom graphs: – spring generation, – autumn generation

The values presented in the last column of Table 15 are the approximate minimum life spans for snails which were never found dead, and maximum, close to actual, life spans for those few individuals which were found dead after the last marking (death indicated by "+" following the date). The estimated life span is compatible with the laboratory results. The average life span in the field was not shorter than 2 years, while for some individuals it exceeded 1,000 days.

LIFE CYCLE

The life cycle of *H. obvoluta* is a 3-year cycle in which the following stages can be distinguished: hatching and growth, adulthood and senility.

Hatching takes place in the spring or autumn which results in two new generations appearing in each vegetation season. The growth to adulthood takes from a few to about a dozen months (most often it is completed next year, in the same season in which hatching took place). The snails attain their ultimate size, and have fully formed lips. Mature snails (maturity can be estimated based on the completed lip, coinciding with mature gonad – MALTZ 2003b) start to reproduce. The number of clutches per lifetime does not exceed six (assuming the maximum life span – in the laboratory the maximum number of clutches was four), only one clutch being laid in each spring or autumn season. Most often the last reproductive season is the one when the snail was hatched (fifth season since maturity), though such an individual can also survive till the next reproductive period and lay eggs. Empty shells devoid of periostracum were the most numerous in the spring and autumn, which indicates a high mortality of senile snails in the summer and during hibernation.

ANNUAL ACTIVITY

In the laboratory and in the field the snails started reproducing in the spring (laboratory March-June, field April-June) and autumn (laboratory September-October, field August-September). In the laboratory they were active throughout the year (feeding, crawling), only in winter periods of inactivity of a few days were observed (aperture covered by a thin epiphragm). In the field the snails hibernated – at the end of October and beginning of November they left the logs and entered cracks in the timber from the underside. They hibernated there with their apertures covered by thick, calcified, "winter" epiphragms. They resumed activity at the beginning or end of April, depending on the weather.

Tabela 14. *Helicodonta obvoluta*. Life span in laboratory (days)

	Life span (days)	Life span (snails brought from the field)	Life span (snails reared in laboratory)
Mean	959.10	952.65	965.75
Standard error	10.26	15.48	13.47
Median	964	950	974
Standard deviation	119.64	128.59	110.24
Variance	14314.17	16536.23	12153.34
Minimum	516	516	738
Maximum	1187	1151	1187
Number of snails	136	69	67

Table 15. Life span estimates based on field observations. A1 followed by an asterisk denotes a subadult individual (lip not completed), + following the date denotes death. For details see text

No.	age class at first marking	date of first marking	estimated time before marking	date of last marking/death	approximate life span
1	A1	05.05.97	548	13.08.97	648
2	A1	19.05.97	548	12.09.97	684
3	A1	05.05.97	548	12.09.97	678
4	A1	05.05.97	548	10.10.97	706
5	A1	13.06.97	548	10.10.97	667
6	A1*	10.10.97	365	17.07.98	645
7	A1	13.06.97	548	17.07.98	947
8	A1*	09.10.98	365	23.04.99	461
9	A1*	24.10.98	365	23.04.99	546
10	A1	09.10.98	548	23.04.99	744
11	A1*	13.08.97	365	23.04.99	983
				23.05.99+	
12	J5	10.10.97	210	23.04.99	870
13	A1	05.05.97	548	23.04.99	1,266
				02.05.99+	
14	A1	11.09.98	548	23.04.99	772
15	A1	24.10.98	548	02.05.99	753
16	A1*	09.10.98	365	02.05.99	768
17	A1	24.10.98	548	02.05.99	753
				06.06.99+	
18	A1*	24.10.98	365	23.05.99	591
19	A1*	24.10.98	365	06.06.99	605
20	A1	10.10.97	548	27.06.99	1,171
21	A1*	23.04.99	365	08.08.99	472
22	A1	11.09.98	548	29.08.99	900
23	A1	09.10.98	548	16.10.99	920
24	A1	16.10.99	548	30.04.00	743
25	J5	18.09.99	210	30.04.00	534
26	A1*	06.09.99	365	30.04.00	693
27	A1	06.06.99	548	30.04.00	876
28	A1*	16.10.99	365	14.05.00	575
29	A1	29.08.99	548	14.05.00	806
30	A1*	18.09.99	365	14.05.00	603
31	A1	16.10.99	548	02.06.00	777
32	A1*	16.10.99	365	02.06.00	594
33	A1	23.04.99	548	02.06.00	953
34	A1	16.10.99	365	01.07.00	623
35	A1	27.06.99	548	01.07.00	907
36	J5	30.04.00	210	05.08.00	307
37	A1*	14.05.00	365	09.09.00	483
38	A1*	02.06.00	365	09.09.00	464
39	A1*	14.05.00	365	29.09.00	503
40	A1	02.06.00	548	29.09.00	667
41	A1	16.10.99	548	29.09.00	1,028

CIRCADIAN ACTIVITY

Activity in constant temperature and humidity conditions

In the laboratory adult snails were very active late in the evening, during the night and early morning (from 20.00 till 8.00), being the most active between 23.00 and 5.00 (Fig. 11). During the day, and especially between 10.00 and 18.00, they stayed in shelters or remained motionless on pieces of rotting timber, but I have not observed a complete retraction to the shell or building epiphragms.

Juveniles were much more active compared to adults. Their activity increased in the afternoon and was maintained till morning (16.00–10.00). During the day, when the adults stayed in their shelters, the juveniles examined the container, fed or stayed on pieces of timber with partly everted tentacles.

Activity in variable temperature and humidity conditions

Contrary to the laboratory snails, the activity of individuals kept in conditions simulating natural clearly depended on the temperature and humidity. Adult snails were active only during the night and early morning (23.00–8.00), the peak activity falling on the period between 3.00 and 6.00 (Fig. 12). During the day the snails sheltered under pieces of timber and remained there till evening. They often closed their apertures with thin epiphragms. Only on the 15/16th July 2000 (Fig. 13) I observed a high activity during the 24 hours, which was associated with a high air humidity (rainy day).

Juvenile snails, like the adults, displayed an increased activity in the night and early morning, and during daytime they also sheltered in rotting timber which was not observed in laboratory conditions.

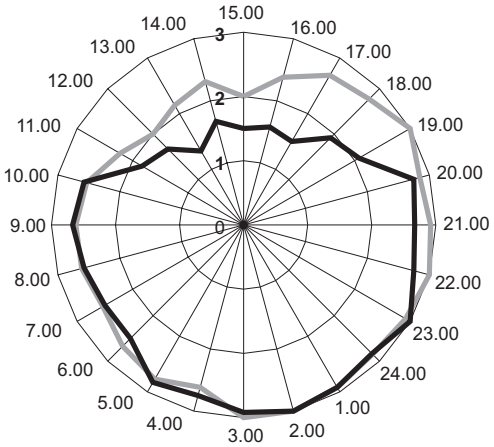

Fig. 11. *Helicodonta obvoluta*. Comparison of mean diurnal activity of juvenile and adult individuals. Constant conditions (1–2 V 2000): grey line – juvenile, black line – adult

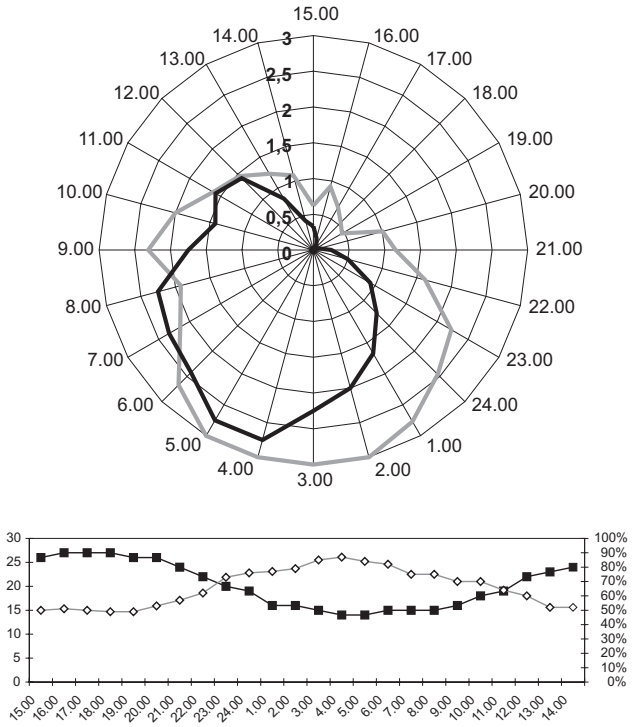

Fig. 12. Comparison of diurnal activity of juvenile and adult *Helicodonta obvoluta*. Variable conditions of humidity and temperature (20–21 V 2000): grey line – juvenile, black line – adult, solid squares – temperature, hollow lozenges – humidity

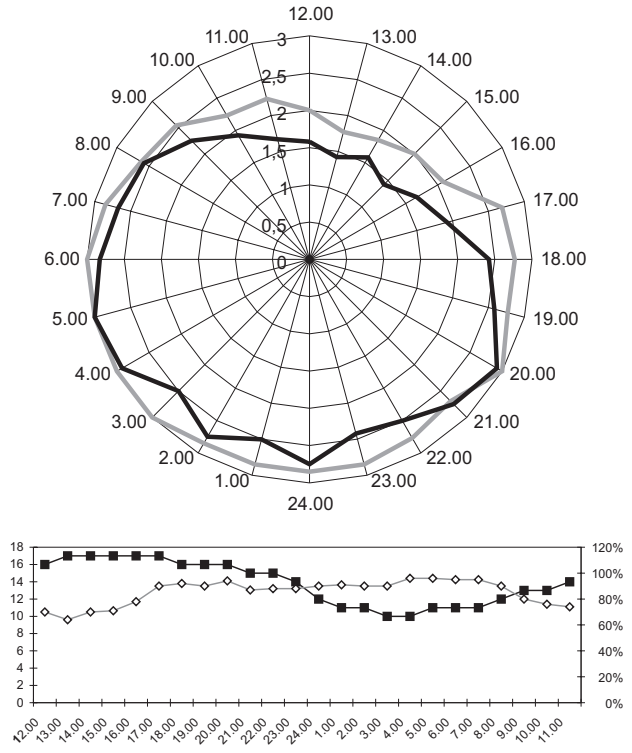

Fig. 13. Comparison of diurnal activity of juvenile and adult *Helicodonta obvoluta*. Variable conditions of humidity and temperature (15–16 VII 2000): grey line – juvenile, black line – adult, solid squares – temperature, hollow lozenges – humidity

MIGRATIONS

In October 1997 and in September 1998, I marked a group of snails (57 and 64 individuals, respectively) collected on logs 35 m away from the study plot. Nine of them were re-captured. Based on the distance covered and the time from the first marking I calculated the migration rate (in case of individuals re-captured after hibernation, the hibernation period was subtracted from the time since the last marking). The distance covered in a month ranged from 3.5 to 8.75 m (mean 6.32, SD=1.50, n=9).

During monthly marking, I re-captured individuals marked in the previous month 4–5, or even 7 metres from the study plot which indicates a rather high mobility.

DISCUSSION

MATING

Mating in pulmonates follows one of two patterns: 1. one of the partners sits on the other's shell which is fairly common in phylogenetically old taxa, e.g. Lymnaeidae, Planorbidae, Ellobiidae (Basommatophora) (MORTON 1954, PURCHON 1977, PIECHOCKI 1979), or Succineidae, Vertiginidae and Endodontidae (Stylommatophora) (JACKIEWICZ 1980, POKRYSZKO 1990b, JACKIEWICZ & ZBORALSKA 1994, KUŹNIK-KOWALSKA 1999); 2. both partners assume the same position which is typical for Arionidae (RIEDEL & WIKTOR 1974, KOZŁOWSKI 2000), Limacidae and Milacidae (WIKTOR 1981, 1989), Agriolimacidae (WIKTOR 1960, 1989, KOSIŃSKA 1980, REISE 1995), Ferrussaciidae (WÄCHTLER 1929), Helicidae (DZIABASZEWSKI 1975, KILIAS 1985, GIUSTI & ANDREINI 1988, BAUR B. & BAUR A. 1992, 1997, KORALEWSKA-BATURA 1999), Bradybaenidae and Clausiliidae (own, unpublished data).

In the former case the position of the snail seems to indicate the role it plays during mating. The top individual plays the part of a male, the bottom one – of a female. Only the top partner everts its male copulatory organs. Such a non-reciprocal copulation has been observed in Lymnaeidae, Planorbidae, Ellobiidae, Succineidae or Vertiginidae (MORTON 1954, PURCHON 1977, PIECHOCKI 1979, JACKIEWICZ 1980, POKRYSZKO 1990b). While in members of the first four families both partners have male copulatory organs and change roles during consecutive copulations, and such behaviour may be regarded as ancestral, in the case of Vertiginidae, though they are phylogenetically old (POKRYSZKO 1990a), the non-reciprocal copulation is probably associated with aphallism (POKRYSZKO 1990b). In *Discus rotundatus* (Endodontidae) the position is similar to that adopted by the snails just named, but the copulation is reciprocal (KUŹNIK-KOWALSKA 1999).

The copulation is preceded by an often complicated courtship dance. Its purpose is mutual recognition: ascertaining species identity and readiness to copulate of both partners. Such behaviour was often observed in the laboratory in *H. obvoluta*, especially when a new snail was introduced into a container where a group of snails had been kept for some time, but after a short recognition resembling the initial stage of courtship dance the snails lost interest in the new individual. Similar relations between snails have been observed, among others, in *Helix pomatia*, *H. aperta* or *H. lutescens* (DZIABASZEWSKI 1975, GIUSTI & ANDREINI 1988, KORALEWSKA-BATURA 1999).

Mating in Helicidae takes place in a horizontal position, when both partners maintain contact of their whole sole with the substratum, or in a vertical position, with their anterior body parts raised perpendicular to the substratum. The horizontal position observed in *H. obvoluta* is typical for *Arianta arbustorum*, *Cepaea nemoralis*, *C. hortensis*, *Tacheocampylea tacheoides*, *Helix aspersa* and *H. aperta* (GIUSTI & ANDREINI 1988, BAUR B. & BAUR A. 1992). The vertical position is assumed by *Eobania vermiculata*, *Helix pomatia*, *H. lucorum*, *H. lutescens* or *Theba pisana* (DZIABASZEWSKI 1975, GIUSTI & ANDREINI 1988, KORALEWSKA-BATURA 1999), but the last species may also copulate in a horizontal position.

Attempts have been made at explaining the diferences in mating positions by environment conditions (GIUSTI & ANDREINI 1988 and literature contained therein). According to GIUSTI & LEPRI (1980 after GIUSTI & ANDREINI 1988) snails of open habitats, i.e. staying on the soil surface, assume vertical position while species living among herbaceous vegetation, shrubs or trees mate horizontally. However, there exist species which do not conform to this rule: *Helix aperta* lives in the former kind of habitat and mates horizontally, while *Theba pisana* living in shrub- or tree-covered habitats can copulate in either position.

Explanation of the position assumed by the mating snails should be sought in the place where the mating occurs: on a horizontal surface (soil, horizontal log) or on branches, leaves etc. which are not horizontal. In such a situation adopting a vertical position, with the anterior body part raised above the substratum, would be impossible or at least difficult. *H. obvoluta*, inhabiting forests, copulates on tree trunks, branches or pieces of timber, and the horizontal position during mating ensures a tight adhesion to the substratum.

In most higher Stylommatophora (Achatinidae, Endodontidae, Arionidae, Zonitidae, Helicidae –

TOMPA 1984, Milacidae – WIKTOR 1981) sperm is transferred in spermatophores. I did not observe such structures either during copulation of *H. obvoluta* or when dissecting adult individuals of the species. SHILEYKO's (1978) conjecture that the folds inside the male copulatory organs of *H. obvoluta* would facilitate spermatophore transfer is thus unjustified. Besides, that author mentions neither the appearance of a spermatophore nor even finding one. The appearance of the white liquid observed to move inside penis during copulation suggests a sperm mass rather than a spermatophore. The situation is the same in e.g. Agriolimacidae (WIKTOR 1989, REISE 1995).

After copulation the snails move apart at once or it is preceded by a resting phase (WIKTOR 1960, 1989, DZIABASZEWSKI 1975, KOSIŃSKA 1980, GIUSTI & ANDREINI 1988, REISE 1995, KORALEWSKA-BATURA 1999). In the case of *H. obvoluta*, after sperm transfer, the partners stay motionless, with their mouths touching, for up to 50 minutes. The resting phase has been observed also in *Helix pomatia*, *H. lutescens*, *H. aperta*, *H. aspersa* or *Theba pisana* (DZIABASZEWSKI 1975, GIUSTI & ANDREINI 1988, KORALEWSKA-BATURA 1999), but in the last three species a full activity just after copulation has also been noted. According to GIUSTI & LEPRI (1980; after GIUSTI & ANDREINI 1988) the presence/absence of resting phase depends on the place of mating. When mating takes place in an open area, reduction of this phase is advantageous since in this way the exposure to e.g. predators, sunlight etc. is minimised. In case of many slugs, both partners show a normal activity immediately after copulation (WIKTOR 1960, 1989, KOSIŃSKA 1980, REISE 1995).

Though the available literature data are scarce, they indicate that the total time of mating varies between species. In Agriolimacidae mating takes from ca. 45 minutes to 6.5 hours (*Deroceras praecox* ca. 45 min., *D. reticulatum* ca. 70 min., *D. rodnae* ca. 2.5 hours, *D. sturanyi* 2–6.5 hours), the sperm transfer taking 30–60 seconds (except *D. sturanyi* – 55–330 minutes) and there is no resting phase (WIKTOR 1960, KOSIŃSKA 1980, REISE 1995). In Helicidae mating lasts on an average from 2 to 5 hours (*Helix lutescens* ca. 3 hours, *H. aperta* 2 hours 40 minutes to 5 hours 5 minutes, *H. pomatia* ca. 4 hours, with sperm transfer of ca. 15 minutes and resting phase of ca. 2–3 hours, *Theba pisana* 1 hour 19 minutes – 3 hours 26 minutes) (DZIABASZEWSKI 1975, GIUSTI & ANDREINI 1988, KORALEWSKA-BATURA 1999). Mating in *H. obvoluta* takes 2–3 hours, with sperm transfer of 10–12 minutes and resting phase of ca. 50 minutes. The fact that various aspects of mating in *H. obvoluta* resemble those in different snails living in different habitats, indicates that such characters have no direct phylogenetic or ecological connotations.

Higher Stylommatophora mate at different times of day: during the day, if temperature and humidity are favourable, e.g. *Deroceras reticulatum*, *D. praecox* or *D. rodnae* (WIKTOR 1960, REISE 1995), in early morning hours, e.g. *Helix aspersa*, *H. pomatia*, or *H. lutescens* (DZIABASZEWSKI 1975, TOMPA 1984, KORALEWSKA-BATURA 1999), or in the night, e.g. *Arion hortensis*, *A. intermedius*, *Limax maximus*, *L. cinereoniger*, *Deroceras sturanyi*, *D. praecox*, *D. rodnae* (RIEDEL & WIKTOR 1974, KOSIŃSKA 1980, TOMPA 1984, WIKTOR 1989, REISE 1995). *H. obvoluta* appears to copulate only in the night which is probably associated with its peak activity at that time.

A comparison of mating behaviour of *H. obvoluta* with that of other members of Helicidae reveals certain similarities and differences. Similarities include the reciprocal copulation, long and complicated courtship dance, horizontal position observed also in *Arianta arbustorum*, *Cepaea nemoralis*, *C. hortensis*, *Tacheocampylea tacheoides*, *Helix aspersa* or *H. aperta* (GIUSTI & ANDREINI 1988, BAUR B. & BAUR A. 1992), and also the resting phase following copulation, like in *H. pomatia*, *H. lutescens*, *H. aspersa*, *H. aperta* or *Theba pisana* (DZIABASZEWSKI 1975, GIUSTI & ANDREINI 1988, KORALEWSKA-BaTURA 1999). *H. obvoluta* has no dart sac, and thus no dart shooting takes place, contrary to the representatives of *Trichia*, *Perforatella*, *Arianta*, *Isognomostoma*, *Helicigona*, *Causa*, *Cepaea*, *Murella*, *Otala*, *Tacheocampylea* or *Helix* (DZIABASZEWSKI 1975, SHILEYKO 1978, TOMPA 1984, KILIAS 1985, GIUSTI & ANDREINI 1988, URBAŃSKI 1989, KORALEWSKA-BATURA 1990, 1993, 1999, BAUR B. & BAUR A. 1992). *H. obvoluta* forms no spermatophores which are typical for helicids (TOMPA 1984). Mating takes place in the night which distinguishes this species from members of the genus *Helix* (DZIABASZEWSKI 1975, TOMPA 1984, KORALEWSKA-BATURA 1999).

EGG-LAYING, INCUBATION, HATCHING

Various kinds of parental care are frequent in snails, especially those exceeding a certain size (BAUR B. 1994 and literature contained therein). They include, among others, placing eggs in rotting timber, in burrows in the soil, and/or covering the clutch with mucus. *H. obvoluta* places its eggs in cracks in rotting wood and covers them with mucus (eggs removed from the timber and placed on another substratum failed to develop). Placing eggs in the timber is no doubt to protect them from desiccation or predators, and to ensure a relatively constant incubation temperature. Ensuring constant temperature and humidity is especially important for snails ovipositing in spring and autumn in the temperate zone, where weather is unstable in these seasons. Covering the clutch with mucus is probably to protect it against microorganisms. The mucus may also contain repelling substances (TOMPA 1984). Members of Helicidae for which the way of egg-laying and parental care have been studied in detail (*Arianta arbustorum*, *Theba*

pisana, *Cepaea nemoralis*, *Helix pomatia*, *H. lutescens*, *H. aspersa*, *H. texta*) (WOLDA 1970, 1972, DZIABASZEWSKI 1975, COWIE 1980, TOMPA 1984, BAUR B. & BAUR A. 1986, HELLER & ITTIEL 1990, KORALEWSKA-BATURA 1999) dig burrows in the soil. These are, however, species living on the soil surface or associated with it. *Causa holosericum* and *Isognomostoma isognomostoma* which, like *H. obvoluta*, live on fallen logs, also lay eggs in rotting timber (own, unpublished data).

The reproductive season in *H. obvoluta* is strictly determined, and both in the field and in laboratory limited to spring and autumn. Slight differences observed between years in the field result from weather conditions. Snails of temperate climate include species of strictly determined reproductive season: *Columella edentula*, *Vertigo pusilla* (POKRYSZKO1990a, b), *Punctum pygmaeum* (RIEDEL & WIKTOR 1974, BAUR B. 1987a, 1989), *Discus rotundatus* (KUŹNIK-KOWALSKA 1999), *Tandonia rustica*, *Limax cinereoniger*, *Malacolimax tenellus, Lehmannia marginata* (WIKTOR 1989), *Deroceras agreste*, *D. reticulatum*, *D. rodne*, *D. praecox* (WIKTOR 1989, REISE 1995), *Cochlodina laminata* (BULMAN 1996), *Vestia elata* (PIECHOCKI 1982), *Alinda biplicata* (KUŹNIK-KOWALSKA 1998a), *Arianta arbustorum* (BAUR B. 1990a, b), *Helix pomatia* (DZIABASZEWSKI 1975, KILIAS 1985), *H. lutescens* (KORALEWSKA-BATURA 1999), and others, reproducing throughout the year: *Carychium tridentatum* (MORTON 1954, BULMAN 1990), *Deroceras leave* (WIKTOR 1989), *Arion subfuscus*, *Arion hortensis* (RIEDEL & WIKTOR 1974).

There are no literature data on the factors determining the onset of reproductive season in snails (TOMPA 1984). The egg-laying in *Lehmannia marginata* and *Deroceras reticulatum* is stimulated by a cephalic ganglia hormone (TAKEDA 1977, 1979), like ovulation in *Helix aspersa* (SALEUDDIN et al. 1983). The data pertain to snails of strictly determined reproductive season, and thus the situation in *H. obvoluta* may be similar. The problem of factors regulating secretion of this hormone remains open (POKORA 1989 and literature contained therein). There are no data on hormonal regulation in snails which are capable of egg-laying throughout the year.

In the case of species inhabiting areas with alternating dry and wet seasons (e.g. Israel, HELLER & ITTIEL 1990, HELLER et al. 1997 and literature contained therein), the activity and reproduction are triggered by the onset of wet season. The stimulating factors are no doubt increase in humidity and/or decrease in temperature. In the temperate zone of Europe, probably such factors as succession of phenological seasons, quantity of precipitation, temperature and the associated food availability, have a significant effect on the snail activity and most probably determine the onset of reproduction in species capable of throughout-the-year reproduction. In such snails as *H. obvoluta*, with a strictly determined reproductive season, both in the field and in laboratory, where the temperature, humidity and food conditions are constant, the decisive factor seems to be the day length. The problem requires further studies. No doubt the environmental factors act through the regulation of hormone secretion affecting the gonad activity and annual cycle of gamete production (POKORA 1989 and literature contained therein, see also MALTZ 2003b).

Fertility and life span are often considered in the context of model strategies r and K. The egg size in *H. obvoluta* is on an average 2.46 × 2.27 mm, which is ca. 20.7% largest shell dimension of adult snail; the mean number of eggs per clutch is 17, during its lifetime an individual can produce 4–6 clutches i.e. 68–102 eggs. The adult shell size is to a large degree corelated with life span (HELLER 1990 and literature contained therein). Corresponding parameters of life cycles of some snails are presented below:

– Small snails [largest shell dimension up to 5 mm]:
a. *Punctum pygmaeum*: eggs laid singly, body: 1.2–1.5 mm, egg: 0.41 × 0.5 mm, eggs per lifetime: mean 6 (BAUR B. 1989);
b. *Vertigo pusilla, Vallonia pulchella*, *Carychium tridentatum*: eggs laid singly, body: mean 1.9–2.5 mm, egg: mean 0.5–0.69 mm, eggs per lifetime: mean 8–30 (WHITNEY 1938, BULMAN 1990, POKRYSZKO 1990b);

– Medium-sized snails [largest shell dimension up to 20 mm]:
a. *Discus rotundatus*: body: mean 6.25 mm, egg: mean 1.1 mm, eggs per clutch: mean 4, eggs per lifetime: mean 32 (KUŹNIK-KOWALSKA 1999);
b. *Cochlodina laminata*: body: 12–20 mm, egg: mean 1.5 mm, eggs per clutch: 1–25, approximate number of eggs per lifetime: ca. 100 (BULMAN 1996);
c. *Arianta arbustorum*: body: 16–20 mm, egg: 2.7–3.2 mm, eggs per season: 20–80 (1–4 clutches), approximate number of eggs per lifetime: ca. 160–320 (BAUR B. 1988a, BAUR A. & BAUR B. 1997);

– Large snails [largest shell dimension over 20 mm]:
a. *Helix texta*: body: mean 40 mm, egg: mean 5.5 mm, eggs per clutch: mean 60 (HELLER & ITTIEL 1990);
b. *Helix pomatia*: body: 40–55 mm, egg: 5.5–8.6 mm, eggs per clutch: 24–93 (mean 50) (DZIABASZEWSKI 1975);
c. *Helix lutescens*: body: 28.1–34.1 mm, egg: 4.0–4.5 mm, eggs per clutch: 16–67, mean 35 (KORALEWSKA-BATURA 1999).

Helicodonta obvoluta can be classified with medium-sized snails.

Small snails, of a life span not exceeding 2 years (reproductive period constitutes ca. 82–93% life span) lay few eggs per lifetime, while large snails, with a life span of several years (reproductive period of ca. 71–86% life span) can produce a considerable num-

ber of eggs which makes the small-sized snails of a shorter life span less fertile, contrary to what would follow from the reproductive strategies r and K (SKELTON 1994).

Such characters of life cycle, as number and relative and absolute egg size, number of clutches per season and per lifetime, as well as life span, seem to be correlated with the adult size rather than with phylogenetic position of the species.

The range of variation of incubation period in *H. obvoluta* is wide (14–31 days). One of factors which may affect the duration of incubation is the ambient temperature, in spite of the clutch being placed in rotting timber which protects it to some degree from temperature changes, though the temperature changes in the laboratory were only slight. The time of incubation of early spring clutches, which was the shortest, indicates that the temperature not exceeding 20°C is close to optimum for the embryo development.

Another factor which may have an effect on the duration of incubation is egg retention in the parent's reproductive system (TOMPA 1979a, b, 1984). The phenomenon has been observed in members of Streptaxidae, Spiraxidae, Achatinidae, Subulinidae, Ferrussaciidae, Helicodiscidae, Systrophidae, Achatinellidae, Valloniidae or Endodontidae (TOMPA 1979a, b, 1984, BAUR B. 1989). Snails capable of egg retention usually lay few eggs (TOMPA 1979a) while strictly oviparous species lay numerous eggs immediately after their formation, e.g. *Limax maximus* or *Helix aspersa*. *H. obvoluta* is most probably strictly oviparous; if there is any egg retention, its duration must be very short. During numerous dissections of adult specimens I found no eggs in their reproductive system.

Hatching in *H. obvoluta* is asynchronous and much extended in time: the time of hatching of a clutch ranges from 1 to 4 days. This results probably from an asynchronous release of the pool of ova from the gonad, as confirmed by the extended time of clutch production, which results in slight differences in the time of syngamy, and the laid eggs differ in the advancement of the initial stages of cleavage (some may contain zygotes, other may contain first blastomere divisions). Such a phenomenon was observed in e.g. *Helix aspersa* (TOMPA 1984). On the other hand, such a mode of hatching may result from the position of eggs in the clutch (eggs placed centrally or peripherally), which may lead to differentiation in the rate of development of the embryos.

Among juvenile *H. obvoluta* I observed no cannibalism, either egg-cannibalism or attacking younger and smaller individuals. The young did not eat the remnants of their egg-shell or dead eggs. The lack of habit of consuming egg-shells may be associated with the mode of hatching. The disappearance of the white egg colour immediately before hatching suggests a usage of resources contained in the egg (Ca, nutritive substances); a young snail is then surrounded only by a thin, translucent membrane, possibly of no nutritive value. Eggs containing dead embryos, with decomposition processes started, are probably recognised as inedible based on chemical stimuli (BAUR B. 1987b, c, 1988b). A similar phenomenon involving dead eggs has been observed in *Deroceras sturanyi* (KOSIŃSKA 1980).

Cannibalism is common among higher stylommatophorans. It has been observed, among others, in *Arianta arbustorum*, *Helix pomatia* (BAUR B. 1987b, c, 1988b, 1990a), *H. lutescens* (KORALEWSKA-BATURA 1999), *Deroceras sturanyi* (KOSIŃSKA 1980), *Discus rotundatus* (KUŹNIK-KOWALSKA 1999). The lack of cannibalistic behaviour in *H. obvoluta* may result from the fact that each clutch is isolated which follows from the egg-laying mode. The earlier hatched juveniles of one clutch have no access to later clutches. However, juveniles of *Arianta arbustorum* and *Discus rotundatus*, both species of asynchronous hatching, like *H. obvoluta*, do not distinguish between eggs of their own and alien clutches, and consume both (BAUR B. 1987c, KUŹNIK-KOWALSKA 1999). In *Arianta arbustorum*, where the clutch is often a result of fertilisation by sperm originating from different partners, the commonality of cannibalism among siblings is explained by the fact that one-clutch siblings are related to a lesser degree than juveniles resulting from fertilisation by the same father. It can be thus supposed that cannibalism is absent or much limited in species where there is no multiple copulation with different partners. It is unknown if such a copulation takes place in *H. obvoluta*. Another explanation postulates that cannibalism is a natural consequence of the habit of consuming the remnants of their own egg envelope by juvenile snails, the snails being unable to distinguish between the empty envelope and still unhatched eggs (BAUR B. 1987b, c). Juvenile *H. obvoluta* have no such habit. Finally, cannibalism could have been selected against in species which are generally not very fertile, since it has not been observed in e. g. *Carychium tridentatum* (BULMAN 1990), *Vertigo pusilla* (POKRYSZKO 1990b), *Vallonia pulchella* (WHITNEY 1938) or *Punctum pygmaeum* (BAUR B. 1987a, 1989).

Observations on individuals of *H. obvoluta* kept in isolation from very early development stages suggest that there is no uniparental reproduction, or that it is very rare. Literature data indicate the absence of such a reproduction in Helicidae. Most authors regard members of this family, e.g. *Arianta arbustorum*, *Cepaea vindobonensis*, *C. nemoralis* and *C. hortensis*, *Helix aspersa* or *H. pomatia* as incapable of uniparental reproduction (FRETTER & GRAHAM 1964 and literature contained therein). In lower pulmonates uniparental reproduction is rather common; this type of reproduction, effected most probably through selfing, is found in members of Lymnaeidae, Planorbidae, Ellobiidae, Succineidae, Vertiginidae, Valloniidae or Endodon-

tidae (WHITNEY 1938, FRETTER & GRAHAM 1964, PIECHOCKI 1979, TOMPA 1984, BAUR B. 1989, POKRYSZKO 1990b, KURNIK-KOWALSKA 1999), and of higher pulmonates in some species of Clausiliidae, Agriolimacidae, Arionidae or Bradybaenidae (RIEDEL & WIKTOR 1974, TOMPA 1984 and literature contained therein, WIKTOR 1989, BAUR B. & BAUR A. 1992, JORDANES et al. 1998).

GROWTH

H. obvoluta grows from hatching till lip formation and sexual maturation, like other helicids (WOLDA 1970, 1972, DZIABASZEWSKI 1975, STAIKOU et al. 1988, HELLER & ITTIEL 1990, BAUR B. 1990b, BAUR A. 1991, BAUR B. & BAUR A. 1992, 1995, KORALEWSKA-BATURA 1999, LIGASZEWSKI 1999).

The fact that snails reared in the laboratory in the first year of culture (progeny of individuals brought from the field) needed, to reach their ultimate size, a much shorter time (mean 354 days spring '97 and 313 autumn '98) compared to those born later (progeny of snails reared in laboratory: mean 442 days spring '99 and 535 days autumn '99) is difficult to explain. The differences were statistically significant (t-test two-sided, $p = 0.000$). Some snails of the '99 generation did not complete their growth. At constant conditions of temperature, humidity and food availability a quick and constant growth should be expected. The only factor which could affect the slowing down of the growth were wintering conditions in the laboratory, quite different from those in the natural habitat.

The differentiated growth rate during the lifetime of snails (rapid initial growth, considerable deceleration in the later period, and a slight acceleration preceding lip formation) is correlated with ontogenetic changes in the gonad (MALTZ 2003b). During the slowed-down growth (stage of 4–5 whorls) intense changes take place in the gonad (increased number of cell divisions, appearance of first gametogonia, their maturation, increasing gonad volume), hence a large part of energy, previously expended on the size growth of the individual, is used for the development of this organ. At the stage of 5 whorls, additionally the growth of other parts of the reproductive system is accelerated which is probably associated with its secretory activity (POKORA 1989 and literature contained therein). Growth acceleration just before lip formation would result from the termination of this energy expenditure (termination of reproductive system development).

Data on the growth rate from field observations indicate that the growth in the earliest stages is the slowest (J3, mean monthly increment 0.35 whorl), it is the quickest at J5 stage (mean 0.5 whorl/month; see also Table 12). These results are not quite compatible with those obtained in the laboratory. In the case of growth in the field, environmental factors should be considered, besides the internal factors. The former may have a significant effect on growth, e.g. variable temperature or humidity associated with the season, hibernation and – during hot and dry summers – aestivation.

There is little literature information on growth rate of terrestrial snails which terminate their growth with attainment of sexual maturity. The rate has been studied, among others, in *Helix pomatia*, *Arianta arbustorum*, *Balea perversa* or *Chondrina clienta* (DZIABASZEWSKI 1975, TERHIVUO 1978, BAUR A. 1990, 1991, BAUR B. & BAUR A. 1992, 1995). Data on their growth were obtained most often in field observations, based on the estimate of population structure. The studies showed a varied growth rate. Though in all the described cases these were seasonal variations, resulting from temperature and humidity changes or limited food resources, the growth curves were similar to those in *H. obvoluta*.

POPULATION AGE STRUCTURE

Studies on seasonal changes of the population age structure make it possible, among others, to ascertain the time of reproduction, growth rate, generation time etc. Many life cycles of terrestrial snails have been described exclusively on the basis of such studies, e.g. *Acicula polita* (DZIĘCZKOWSKI 1972), *Cochlicopa lubrica* (UMIŃSKI & FOCHT 1979), *Columella* spp. (POKRYSZKO 1987), *Chondrina clienta* (BAUR B. & BAUR A. 1995), *Arion* spp. (RIEDEL & WIKTOR 1974), members of Vitrinidae (UMIŃSKI 1975, 1979, 1983, UMIŃSKI & FOCHT 1979), *Tandonia rustica*, members of Agriolimacidae and Limacidae, *Boettgerilla pallens* (WIKTOR 1989), *Euconulus fulvus* (UMIŃSKI & FOCHT 1979), *Vestia elata* (PIECHOCKI 1982), *Alinda biplicata* (KUŹNIK-KOWALSKA 1998b), *Balea perversa* (BAUR A. 1990, BAUR B. & BAUR A. 1992), *Bradybaena fruticum* (STAIKOU et al. 1990) or *Cepaea nemoralis* (WOLDA 1970, 1972). In case of *H. obvoluta* such studies made it possible to ascertain: spring and autumn reproduction, wintering growth stages, growth rate of individuals at particular growth stages, generation time and life span.

Both in the laboratory and in the field, *H. obvoluta* reproduces in spring and autumn, while the differences involve the growth rate and life span. In the laboratory, in close-to-optimal conditions, the growth rate is affected only by internal factors, associated with the gonad development. In the field the growth rate is additionally modified by environmental factors. Life span is also dependent on the living conditions of the snails: in the laboratory the life span is close to maximal, resulting from the snail's biology, whereas in the field it is an actual life span depending on ecological factors. The fact that adult individuals dominated in each sample suggests overlapping of adult generations of at least two years (cf. Fig. 10).

LIFE SPAN

The life span of *H. obvoluta* in the laboratory, under constant temperature, humidity and food conditions, was longer than that observed in the field. Such a regularity has been observed also in other species which were studied in parallel in the field and in the laboratory: *Vertigo pusilla*, *Deroceras sturanyi* or *Discus rotundatus* (KOSIŃSKA 1980, POKRYSZKO 1990b, KUŹNIK-KOWALSKA 1999). This is associated with the prolongation of the time elapsing between the last egg laid and death; in the field this time is usually very short (KOSIŃSKA 1980). In snails growing throughout their life, especially slugs, this period involves further growth which was considerably inhibited during sexual activity.

LIFE CYCLE

The life cycle of *H. obvoluta* lasts 3 years. Hatching takes place in spring or autumn (2 generations produced in each vegetation season). In 6–15 months the snails reach sexual maturity, and their shells have clearly developed lips. They start reproduction, producing up to six clutches per lifetime (68–102 eggs), one clutch (9–27 eggs) in the spring, and one in the autumn reproductive season. The time of reproductive life ranges from ca. 1 to 2 years. After laying the last clutch senile period starts. The cycle can be described as medium-long, with a rather short time of growth and maturation which constitutes ca. 1/3 life span, and a fairly long period of reproductive life, of ca. 2/3 individual life.

Cycles of similar duration and of similar parameters have been found, among others, in *Cochlicopa lubrica*, *Euconulus fulvus* (UMIŃSKI & FOCHT 1979), *Discus rotundatus* (KUŹNIK-KOWALSKA 1999), *Tandonia rustica*, *Limax cinereoniger*, *Limax maximus* (WIKTOR 1989) and of helicids: *Helicella itala* (HÄNSEL et al. 1999) or populations of *Arianta arbustorum* from western Europe (TERHIVOU 1978).

Another group of life cycles includes short cycles – the life span ranges from a few to about a dozen months (most often 1–2 years), quick maturation (one to a few months), and the reproduction lasting for about a year. Species of such life cycles include, among others, *Acicula polita* (DZIĘCZKOWSKI 1972), *Carychium tridentatum* (BULMAN 1990), *Vertigo pusilla* (POKRYSZKO 1990b), *Vallonia pulchella* (WHITNEY 1938), *Punctum pygmaeum* (BAUR B. 1989), *Arion rufus*, *A. subfuscus*, *A. hortensis* (RIEDEL & WIKTOR 1974), *Vitrina pellucida*, *Semilimax* spp. (UMIŃSKI 1979, UMIŃSKI & FOCHT 1979), *Deroceras sturanyi* (KOSIŃSKA 1980), *D. reticulatum*, *D. praecox*, *D. laeve* (WIKTOR 1989), and of Helicidae *Candidula unifasciata* (HÄNSEL et al. 1999).

The third category includes long life cycles (life span over 4 years, with individual cases of 14–15 years) (BAUR B. 1988a, HELLER & ITTIEL 1990). Maturity is reached in 2–4 (5) years, and the reproduction lasts several years. Examples of snails of long life cycles are: *Chondrina clienta* (BAUR B. & BAUR A. 1995), *Lauria cylindracea* (HELLER et al. 1997), *Alinda biplicata* (KUŹNIK-KOWALSKA 1998a), *Vestia elata* (PIECHOCKI 1982), *Bradybaena fruticum* (STAIKOU et al. 1990), *Arianta arbustorum* (TERHIVOU 1978 – populations from Finland, BAUR B. & RABOUD 1988) or species of the genus *Helix* (DZIABASZEWSKI 1975, KILIAS 1985, STAIKOU et al. 1988, HELLER & ITTIEL 1989, KORALEWSKA-BATURA 1999).

Only small snails (e.g. *Carychium*, *Vertigo*, *Vallonia*, *Caecilioides*, *Punctum* etc.) or slugs/semislugs (Vitrinidae, Arionidae, Agriolimacidae) display short life cycles. An exception is e.g. a medium-sized snail *Candidula unifasciata* (HÄNSEL et al. 1999). It is a thermophilous species and perhaps this is the explanation of a short life cycle, atypical of helicids. Numerous medium- or large-sized species with thick shells have longer life cycles and reproduce for more than one season. The group includes also some exceptions: slugs Milacidae and Limacidae, and small snails, e.g. *Lauria cylindracea,* whose rather long life cycle (4–5 years) results probably from ovoviviparity and climate-imposed seasonality of reproduction.

ANNUAL ACTIVITY

H. obvoluta is a forest-dweller of the temperate climate of Europe, with alternating seasons and variable humidity and temperature. This affects the annual activity of the species. In the annual cycle, periods of intense activity fall on spring and autumn. In summer the activity decreases, in winter the snails are inactive. Resumption of activity in spring depends on the weather conditions and takes place at the end of March or in April. The snails feed and start reproducing (April till the end of June). At that time both juvenile and adult snails are active till late morning, besides the typical nocturnal activity periods. With the onset of summer they become less active and since late morning till evening they remain in shelters. In late summer and autumn the activity pattern is similar to that in spring, while the autumn reproduction, depending on weather conditions, lasts from the end of August till the first days of October. In the first decade of October *H. obvoluta* leaves the logs where it stayed since spring, and enters the litter close to the logs, seeking hibernation shelters. The hibernation in rotting logs lasts from the end of October till the beginning of April. The snails enter cracks in the rotting timber from the underside of logs. The hibernation logs are logs of adult trees and are in an advanced stage of decomposition. In Great Britain, in a climate with much milder winters, the species winters in leaf-litter, rarely in rotting timber (CAMERON 1972).

CIRCADIAN ACTIVITY

Circadian activity of juvenile individuals, much higher compared to adults, in both natural and laboratory conditions, can be explained by higher energy and food requirements implied by growth.

Adult and juvenile individuals showed an increased activity in late evening and night, as well as in early morning, both in natural conditions and in the laboratory. Under variable humidity and temperature conditions the peak activity of adult individuals fell on the period from 3.00 to 6.00, in the laboratory from 23.00 to 5.00, in the case of juveniles the respective periods were from 23.00 to 8.00 and from 16.00 to 10.00. The reasons for changes in the diurnal activity may be intensity of sunlight (the only factor which was variable in laboratory conditions), temperature and humidity. During the rain active snails were observed also during daytime.

Similar results have been obtained in the studies on circadian activity of *Deroceras sturanyi* (KOSIŃSKA 1980 and literature contained therein) and *Helix lutescens* (KORALEWSKA-BATURA 1999 and literature contained therein). A distinct effect of such factors as light, humidity and temperature on the snail activity has been noted. Besides the environmental factors, a significant factor determining the activity is the internal rhythm of organism activity, independent from external factors (see KOSIŃSKA 1980 for literature review). However, it follows from the observations that atmospheric factors and the intensity of sunlight have a significant effect on the animals, but it can be supposed that circadian rhythm is a resultant of the effect of external factors and the animal's internal clock.

MIGRATIONS

H. obvoluta is rather mobile (covering a mean distance of 5–9 metres per month). The migrations were especially intense in spring, when the snails were leaving the cracks in rotting timber where they had hibernated, and in autumn when they were seeking hibernation shelters (re-captures were 3–5%). During the vegetation season *H. obvoluta* stays mainly on rotting logs which results in a low intensity of migration in that period. An additional confirmation is found in the results of monthly marking of snails staying on one log, where the re-captures were ca. 15%.

Knowing biology and the annual and diurnal activity of *H. obvoluta*, such a behaviour is easily explained. The snails are associated with rotting logs, inside which they find shelter, lay eggs and hibernate. Plants and fungi developing on the surface of the logs constitute their food. As a result snails migrate in search of food, sites for egg-laying or mating partner. It should be also pointed out that during the vegetation season the snails stay on the logs in a rather high density (from May till September the monthly collection of snails during two hours from a log ca. 9 m long often exceeded 100 individuals).

Fallen logs and smaller pieces of timber constitute a complicated system enabling migrations of snails all over the forest floor, ensuring contact between all the individuals in the population and the possibility of invading new areas. In late spring, summer and early autumn this is the only way of migration. Snails are found in litter only in early spring and late autumn which is associated with leaving or seeking hibernation shelters.

The above observations are compatible with the results of the studies on the density and species composition of the malacofauna in litter samples, taken in four seasons of the year in the nature reserve Muszkowicki Las Bukowy (KUŹNIK-KOWALSKA 1998b). In spring and summer samples only single individuals were found, whose percentage in the whole litter malacofauna increased insignificantly in autumn, while in winter samples no *H. obvoluta* was found which excludes its ability to hibernate in the litter.

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