

# Influence of egg cannibalism on growth, survival and feeding in hatchlings of the land snail *Helix aspersa* Müller (gastropoda, pulmonata, stylommatophora)

C Desbuquois

Laboratoire de zoologie et d'écophysiologie, UA Inra/UMR 6553 du CNRS,  
Faculté des sciences, université de Rennes 1, avenue du Général Leclerc,  
35042 Rennes cedex, France

(Received 10 September 1996; accepted 26 November 1996)

**Summary** — Under controlled conditions, growth, survivorship and several nutritional parameters (ingestion, egestion and assimilation) were measured weekly in hatchlings that either ate a conspecific egg after birth (cannibalistic) or not (non-cannibalistic) and in food-deprived individuals (control group). Subsequently, the snails were fed on *Taraxacum officinale*. After 4 days, cannibalistic snails were 1.3 times heavier than food-deprived snails and 100% survived (75.8% in the control group and 40% of the non-cannibalistic individuals). Mortality, particularly in smaller snails, might be a consequence of food deprivation. Nutritional and energetic gains of oophagy increased both future survivorship and growth. After 11 weeks, cannibalistic snails were 1.4 times heavier and had higher survival rates than food-deprived ones although ingestion, egestion rates and assimilation efficiency were similar in both groups. The larger wet weight of cannibalistic snails after 4 days induced a higher food consumption and thus a higher growth rate. The influence of oophagy on life-history traits is discussed in relation to costs and benefits.

**nutrition / *Helix aspersa* / egg cannibalism / growth / survival**

**Résumé** — Influence du cannibalisme des œufs par les nouveau-nés sur la croissance, la survie et la nutrition chez l'escargot petit-gris *Helix aspersa* Müller (gastéropode, pulmoné, stylommatophore). En condition contrôlées, la croissance, la survie et plusieurs paramètres nutritionnels (ingestion, excrétion et assimilation) sont mesurés chaque semaine chez de jeunes *H aspersa* qui, pendant 4 jours suivant l'éclosion, ont consommé un œuf de cette espèce (cannibales) ou non (non can-

---

\* Correspondence and reprints.

Tel: (33) 02 99 28 61 56; fax: (33) 02 99 28 16 12; e-mail: secretariat-zoo-ecophy@univ-rennes1.fr

nibales) et chez des individus ayant jeûné (témoins). Pendant 11 semaines, des feuilles de *Taraxacum officinale* sont utilisées comme aliment. Après 4 jours, les individus cannibales sont 1,3 fois plus lourds que les individus ayant jeûné et 100 % ont survécu (contre 75,8 % des témoins et 40 % des non cannibales). La mortalité affecte particulièrement les petits individus. Les apports nutritionnel et énergétique de l'oophagie permettent une survie et une croissance plus importantes. Après 11 semaines, les individus oophages sont 1,4 fois plus lourds et présentent une meilleure survie que les escargots ayant jeûné. Les taux d'ingestion, d'excrétion et le rendement d'assimilation sont similaires. Ainsi, le poids plus élevé des individus oophages après 4 jours provoque une ingestion supérieure ultérieurement et donc une plus forte croissance. Les individus ayant jeûné pendant 4 jours ne peuvent pas compenser leur retard de croissance. L'influence du cannibalisme des œufs sur « l'histoire de vie » est discutée en relation avec ses coûts et bénéfices.

**nutrition / *Helix aspersa* / cannibalisme des œufs / croissance / survie**

## INTRODUCTION

The number of individuals surviving to the adult stage is a crucial factor in the dynamics of populations. Therefore juvenile survival is very important and may be affected by intraspecific predation, ie, cannibalism. One type of cannibalism, namely oophagy, which concerns the consumption of unhatched eggs by hatchlings (Polis, 1981), has been studied in some land snail species (Baur, 1988, 1990a, b, 1992, 1994a; Baur and Baur, 1986).

In the land snail *Helix aspersa* Müller, Elmslie (1988) had noted that newly hatched snails may exhibit egg cannibalism. In this species, eggs were laid in humid earth in a depth of some centimetres. A hatching asynchrony exists among eggs of the same clutch. This factor could promote oophagy as demonstrated in *Arianta arbustorum* L (Baur and Baur, 1986). This phenomenon, combined with the period of time during which hatchlings remained in their nest after hatching – 6 days on average – (Herzberg and Herzberg, 1962) might allow first born snails feeding on unhatched eggs in the nest (sibling cannibalism). In preliminary experiments, this feeding behaviour appeared to be common in *H aspersa* and to occur in relation to some proximate factors (Desbuquois and Madec, in preparation).

The aim of the present study is to carry out a quantitative investigation of the bene-

fits of egg cannibalism (on growth and survival) in newly born *H aspersa*. To highlight the effect of egg cannibalism, which might be hidden by nutrition differences between cannibalistic hatchlings and non cannibalistic/control animals during their growth, I measured different nutritional parameters: feeding ingestion and faecal egestion. Oophagy cannot be studied with egg-clutches kept in the soil because numerous uncontrolled factors might influence the eggs' development under these conditions and a single snail might cannibalize several eggs in the hatch. Thus, this experiment took place in small aluminium capsules, without earth and under controlled conditions.

## MATERIALS AND METHODS

### Biological materials

Adults of the land snail *H aspersa* were collected from salt-pans at Guerande (South Brittany, in France) and reared under the following conditions to promote reproduction: temperature: 20 °C  $\pm$  1; relative humidity: 80%  $\pm$  5; photoperiod: 18/6 (L/D). Eggs, laid in humid earth, were washed before use. During 11 weeks, food consisted of small discs (13 mm in diameter) of leaves of *Taraxacum officinale* (Weber). The plants were collected in the wild before use. They were cut in the lamina without veins with a cork borer. *T officinale* is known to be highly palatable for *H aspersa* and is abundant in numerous biotopes of this species. Moreover, this natural

food had induced a low variability in the growth of *H. aspersa* in preliminary experiments (Desbuquois, 1991).

### Experimental conditions

A single hatch of *H. aspersa* was divided into two groups of equal size. One group was incubated at 20 °C to obtain hatchlings for the tests and the other at 15 °C to slow down the embryonic development of eggs which were used to feed animals of the treatment group (Baur, 1988, 1990a, 1994a; Baur and Baur, 1986). According to Le Calve (1987), these conditions induce a hatching delay of about 9 days for the eggs incubated at 15 °C. When the eggs incubated at 20 °C hatched, each newborn snail was weighed and placed individually in a small aluminium capsule (height: 6 mm; diameter: 20 mm; surface: 10.1 cm<sup>2</sup>).

Two sets of replicates were constituted: hatchlings were fed with a conspecific egg ( $n = 43$ ; treatment) or received neither an egg nor any other food item ( $n = 33$ ; control group). In natural conditions, hatchlings can feed on organic matter present in the earth, but cannot consume plants because they remain several days in their nest after hatching. I decided not to feed the control group, because cannibalistic snails might equally consume earth and the aim of our experiment was to test and measure the effect of cannibalism only. In any case, in my preliminary laboratory experiments, hatchlings had not consumed organic matter when remaining into the soil during 4 days. Eggs used as food were weighed before being given to snails. During the first 4 days of their life, snails were maintained in plexiglass boxes in darkness at a temperature of 20 °C and a humidity of 100%. In the group of snails which had the possibility of cannibalizing one egg, I observed each day the degree of egg consumption. On the 4th day, all surviving snails in the treated and control groups were weighed to evaluate the weight increase during the first 4 days of their life. The remains of the eggs offered as food were collected, dried in a freeze-drying apparatus and then weighed again. In the same way, eggs of two clutches were weighed, dried to constant weight and weighed again to study the regression between wet and dry weights of eggs. The use of this regression allowed us to know the dry weight of each egg consumed and to cal-

culate the egg consumption of each cannibalistic snail.

Then each snail of both groups was placed in a separate Petri dish (height: 11 mm; diameter 88 mm; surface: 152.1 cm<sup>2</sup>) under the same conditions as before except for photoperiod: 16/8 (L/D)-chosen to be similar to natural one in spring. During 11 weeks, I tested the influence of early egg cannibalism on the subsequent growth, survival and nutrition of the snails in relation to starved snails. Petri dishes were sprayed with distilled water twice a week. During the first 4 weeks, one disc of leaf was given per week to each snail; from week 5 to 9, two discs, and from week 10 to 11, four discs per week. All the discs were weighed before being given to the snails.

Each week, snails from both treatment groups were food-deprived during the first 3 days and *T. officinale* leaf discs were given during the 4 last days. Faeces were removed the 3rd day of the following week, so that digestion was achieved and faeces derived from the 4 days' previous feeding. Several wet discs of *T. officinale* were weighed, dried to constant weight and weighed again so that a regression between wet and dry weight of *Taraxacum* discs could be calculated.

### Parameters used

Once a week, the number of surviving snails was counted and the live weight (LW in mg) of each of them was measured. This measure is a sufficient parameter to estimate the growth of young *H. aspersa* (Lucarz and Gomot, 1985). At the end of the experiment, the animals' shell diameter was measured. Then, all surviving individuals were killed; shells and bodies were separated before being dried to constant weight by freeze-drying and weighed again.

According to Lamotte and Stern (1987) and Davies et al (1990), the energy budget equation is:  $C = A + NA$  with  $A = Pg + Pr + R + M$  and  $NA = F + U$  where  $A$  = quantity of energy assimilated,  $C$  = food consumption or ingestion,  $F$  = faecal egestion,  $M$  = mucus secretion,  $NA$  = quantity of energy not assimilated,  $Pg$  = somatic growth,  $Pr$  = reproductive investment,  $R$  = respiration and  $U$  = urine excretion. In our experiment, reproductive investment is nil (because our snails were in the growth phase and did not invest energy in reproduction). Like numerous authors (Mason, 1970; Charrier and Daguzan, 1980; Seifert and Shutov, 1981; Lazaridou-Dim-

itriadou and Kattoulas, 1991), urine excretion was considered with faeces and not measured precisely. The simplified equation used was:  $C = A + F$ . Thus, assimilation could be inferred.

Each week, the uneaten remains of leaf discs were collected and the area eaten was calculated by measuring the remaining area and subtracting it from the initial one. The remaining area was estimated by drawing a disc (13 mm in diameter) on a plexiglass plate divided radially and in a circle into 64 equal areas. I observed each partially eaten leaf disc on this grid under  $12.5 \times$  magnification. The leaf area consumed was converted into the amount of wet weight consumed and then into the amount of dry weight using the regression equation between wet and dry weights so as to assess the food consumption (C) in mg dry weight of food/individual/week. The rate of consumption (C/LW) is the food consumption divided by the live weight of the animal.

Faecal egestion (F) was measured by collecting faeces produced per animal during a week and is expressed in mg dry weight of faeces/individual/week. The rate of egestion (F/LW) is the faecal egestion divided by the live weight of the snail. Faeces produced during the 4 days of cannibalism were not removed because of their extremely small weight.

Assimilation rate was obtained by subtracting the rate of egestion from the rate of consumption. The assimilation efficiency (CUD, in percent) was calculated for both groups according to the age of snails. It was defined as dry weight of food consumed (mg/individual/week) – dry weight of faeces produced (mg/individual/week)  $\times 100$  / dry weight of food consumed.

### Calorimetry

To determine the calorimetric equivalents of leaves of *T officinale*, faeces and snails' bodies, these materials were burned in a bomb calorimeter (Par) with platinum capsule and fuse. Several leaves of *Taraxacum* and egg clutches of *H aspersa* were used [the dry weight of material used was  $203.3 \pm 18.1$  mg (range: 183.3 – 229.4) for eggs and  $154.1 \pm 28.9$  mg (range: 115.8 – 184.0) for *T officinale*]. At the end of the experiment, bodies of cannibalistic snails were put together to obtain sufficient material (non-cannibalistic/control snails could not be used because of technical problems which prevented

us from obtaining any calorific value). Concerning snail faeces, the study dealt with cannibals and non-cannibals/controls faeces at different ages (after 60, 74 and 81 days). At first, materials were dried, reduced to powder and compressed in pastilles with a pellet press. These pastilles were burned and the calorific energy released was measured. The calorimeter was standardized with benzoic acid.

### Statistical analyses

Because of the small number of surviving snails among non-cannibalistic individuals (snails which had not consumed the available egg) and no significant differences with control snails, growth and nutritional values of these two groups were combined in statistical analyses and figures, but their survivorship was considered separately.

Data were analysed using STATVIEW (1988) software for Macintosh, BIOMEKO (1992) and STATITCF (1991) for MS-DOS. Statistical analyses were based on Sokal and Rohlf (1981), Scherrer (1984) and Zar (1984).

Temporal changes in individual values were examined according to egg cannibalism using multivariate analysis of variance (MANOVA) and Roy-tests. These repeated measures were not independent because they were made on the same individuals. Normality, using tests of kurtosis and symmetry (coefficients of K Pearson) on the residuals and homogeneity of variances of the residuals (Bartlett test) were checked. It required the same number of replicates in the cannibalistic and the non-cannibalistic/control groups. Thus, in performing these analyses, I used only 17 of the 22 surviving cannibalistic snails after 81 days (to obtain equal numbers of individuals in the two groups); they were selected to be representative of the growth curve (mean and variance) obtained with all the cannibalistic snails.

One-way ANOVA were computed and followed by Newman-Keuls multiple comparison tests to detect significant growth differences according to age.

Linear single or multiple regressions were computed when conditions of normality and variance homogeneity were respected. I verified whether the distribution of residuals was normal (using Lilliefors test).

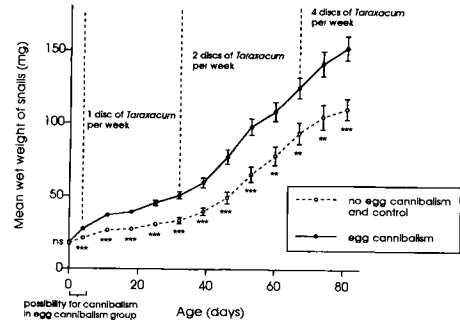
Student *t*-tests (unpaired, two tailed) or Mann-Whitney tests were used to compare the means in the case of two modalities. A non parametric Spearman's rank correlation was used when values were not distributed normally.

## RESULTS

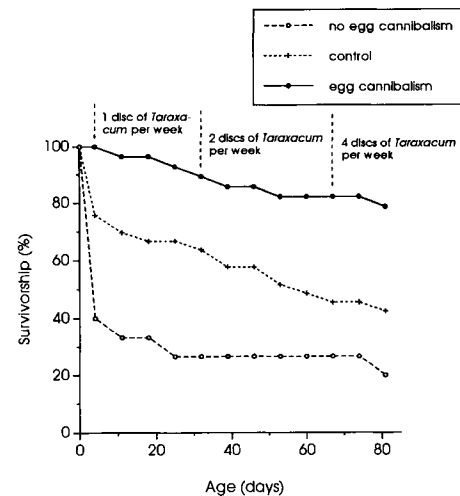
### Rate of egg cannibalism, growth and mortality during the first 4 days of life

Of a total of 43 hatchlings tested for their cannibalistic propensity, 28 (65.1%) cannibalized entirely or partially the egg offered. Only seven (16.3%) of the snails consumed the whole egg. Thus, under the present experimental conditions, egg predation occurred frequently. Among potentially cannibalistic snails, there was no difference in live weight at the beginning of the experiment between those hatchlings which cannibalized the egg and those which did not (Mann-Whitney test;  $Z = -1.73$ ;  $P = 0.83$ ). Hence, egg cannibalism did not seem to be influenced by the weight of hatchlings. Furthermore, there was no difference in wet weight between snails from the treatment group and the control group at the hatching stage ( $17.51 \pm 0.45$  mg; mean  $\pm$  SE) (*t*-test;  $P = 0.61$ ). After 4 days on different diets, cannibals weighed  $27.31 \pm 0.77$  mg, while non-cannibals weighed  $21.52 \pm 1.45$  and controls  $20.85 \pm 0.68$  mg. The difference between controls and non-cannibals was not significant (*t*-test;  $P = 0.67$ ). So, cannibalistic snails grew 1.3 times faster than non-cannibalistic/control snails within 4 days (fig 1).

After the first 4 days of experiment, 75.8% of the control snails survived, but only 40% of the group which had not fed on the available egg (fig 2). Among the food-deprived snails, those which died were smaller than the surviving ones (Mann-Whitney test;  $Z = -2.29$ ;  $P = 0.02$ ), although no differences were noted between control and non-cannibalistic snails. On the other hand, no mortality occurred in the group of



**Fig 1.** Growth of the land snail *Helix aspersa* during the 11 weeks following a 4-day period of egg cannibalism (continuous line;  $n = 28$ ) or starvation (dashed line;  $n = 31$ ). Error bars indicate standard error. Vertical dashes indicate a change in food quantity. ANOVA: ns:  $P > 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ .



**Fig 2.** Survival of cannibalistic and non-cannibalistic hatchlings of *Helix aspersa* in relation to age. In the cannibalistic ( $n = 28$ ) and non-cannibalistic ( $n = 6$ ) groups, one egg was offered to each snail during the first 4 days of life. In the control group ( $n = 25$ ), no food was given during this period. Vertical dashes indicate a change in food quantity.

cannibalistic hatchlings during the 4-day period of egg-eating.

## Growth rates

Egg cannibalism enhanced greatly the growth rate of snails (fig 1): after 81 days, the wet weight of initially cannibalistic snails was 1.38 times greater than that of non-cannibalistic and control snails (wet weight of cannibals:  $152.08 \pm 8.15$  mg, non-cannibalistic/control snails:  $110.08 \pm 7.17$  mg). However, no difference in the within-group variation of growth rate was found after 81 days. In the two groups, shell diameter and wet weight at the end of the experiment were highly correlated (Spearman's rank correlation;  $r_s = 0.85$ ;  $n = 22$ ;  $Z = 3.9$ ;  $P = 0.0001$  for cannibalistic hatchlings and  $r_s = 0.84$ ;  $n = 17$ ;  $Z = 3.34$ ;  $P = 0.0008$  for non-cannibalistic/control snails).

The two groups differed significantly in wet weight at all ages, except at the beginning of the experiment (ANOVA;  $P < 0.01$ ). Age had a significant effect on wet weight (MANOVA;  $F = 75.75$ ;  $P < 0.001$ ). Furthermore, an interaction between egg cannibalism and age was noted (Roy-test;  $P < 0.001$ ).

## Survival

Oophagy also influenced the survival of snails (fig 2). In the cannibalistic group, 78.6% of the animal survived until day 81 compared with 20% of snails which had not cannibalized the available egg and 42.4% of the control animals. In all three groups, the proportion of surviving snails decreased with age. However, mortality rate increased more rapidly in the non-cannibalistic group than in the control group. No influence of the number of *Taraxacum* discs offered on the survival rate could be found.

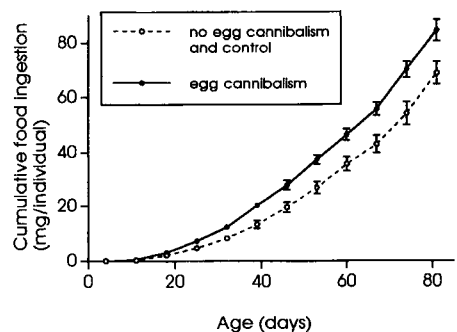
## Feeding ingestion

Dry and wet weights of discs cut in leaves of *Taraxacum* were highly correlated. The lin-

ear regression that describes this relation is: dry weight (mg) = 0.23 wet weight (mg) - 0.13 ( $n = 50$ ;  $r^2 = 0.74$ ;  $F = 134.1$ ;  $P = 0.0001$ ).

When consumption was evaluated in mg dry food consumed per animal and per week (cumulative values during the period of growth until 81 days), the difference between the two groups was significant (Mann-Whitney test;  $Z = -3.23$ ;  $P = 0.001$ ) (fig 3). After 11 weeks, cannibalistic snails had ingested a larger amount of *Taraxacum* leaves than non-cannibalistic/control hatchlings ( $84.45 \pm 3.92$  mg and  $68.68 \pm 4.11$  mg of food in dry weight per individual, respectively).

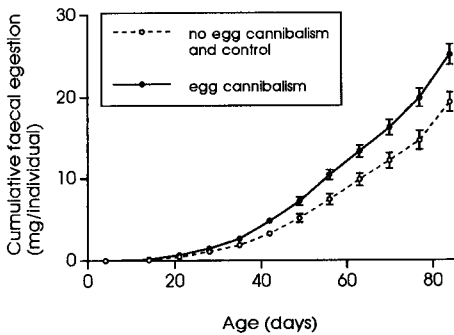
Ingestion rates varied between 0.01 and 0.12 mg dry weight of leaves. $\text{mg}^{-1}$  live weight of snail. $\text{week}^{-1}$  (fig 5) and were influenced by age (MANOVA;  $F = 39.10$ ;  $P < 0.0001$ ), but the differences of ingestion rates between cannibals and non-cannibalistic/control snails were not significant in relation to age (Roy-test;  $P = 0.28$ ). No reasons could be found to explain ingestion fluctuations according to age. No relationship was found between the variation in the amount of food available and the rate of ingestion.



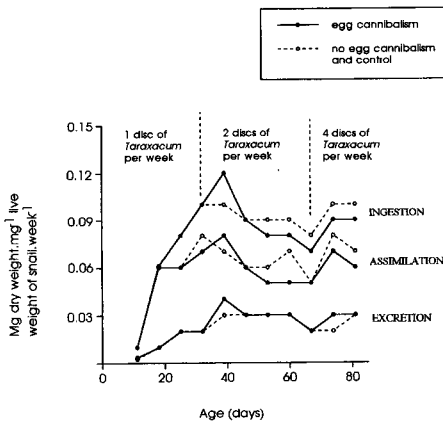
**Fig 3.** Effect of egg cannibalism during the first 4 days of life on the cumulative food ingestion over 81 days in hatchlings of *Helix aspersa*. Error bars indicate standard error.

## Faecal egestion

Like consumption, cumulative faecal egestions were different in the two groups (Mann-Whitney test;  $Z = -3.31$ ;  $P = 0.001$ ). After 81 days, cannibals egested  $25.15 \pm 1.22$  mg dry weight of faeces per individual and non-cannibalistic/control only  $19.32 \pm 1.22$  mg (fig 4). Egestion rates were



**Fig 4.** Effect of egg cannibalism during the first 4 days of life on the cumulative faecal egestion over 81 days in hatchlings of *Helix aspersa*. Error bars indicate standard error.



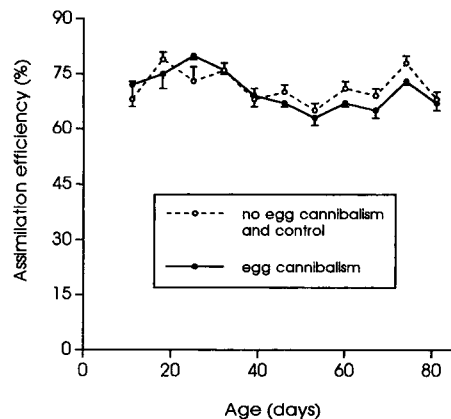
**Fig 5.** Changes in weekly ingestion, egestion and assimilation rates of *Taraxacum officinale* by *Helix aspersa* from different treatment groups. Vertical dashes indicate a change in the amount of food offered.

influenced by age (MANOVA;  $F = 61.00$ ;  $P < 0.0001$ ), but there was no interaction between cannibalism and age factor (Roy-test;  $P = 0.45$ ). Thus, no significant differences were observed between the two groups in relation to age (fig 5).

## Assimilation

The assimilation rate increased with time between the first 32 days and then varied between  $0.01 \pm 2.4 \cdot 10^{-3}$  and  $0.08 \pm 0.01$  until an age of 81 days (MANOVA;  $F = 32.57$ ;  $P = 0.0001$ ). The differences between the two groups were not significant (Roy-test,  $P = 0.22$ ) (fig 5). In the two groups, the CUD coefficient varied little with the age of snails (fig 6).

I observed an increase in the assimilation efficiency during the first 3 weeks, then a decrease until the 7th week and again an increase until the 10th week (MANOVA;  $F = 14.34$ ;  $P = 0.0001$ ). The two curves were not significantly different from each other (Roy-test;  $P = 0.22$ ).



**Fig 6.** Changes in assimilation efficiency of *Taraxacum officinale* by *Helix aspersa* from different treatment groups. Error bars indicate standard error.

## Calorimetry

The calorific value of eggs and *T officinale* were similar (Mann-Whitney test;  $Z = -0.52$ ;  $P = 0.60$ ) although the ash content of eggs was higher (Mann-Whitney test;  $Z = -2.61$ ;  $P = 0.009$ ); the one of faeces was a little higher than *T officinale* energetic value (Mann-Whitney test;  $Z = -2.74$ ;  $P = 0.006$ ) (table I). No differences in faeces energetic equivalents were found between the two groups (Mann-Whitney test;  $Z = -0.22$ ;  $P = 0.83$ ), probably because of the same assimilation efficiency. Thus, I did not convert the values of weight into energy.

The linear regressions between wet and dry weights of eggs from the two clutches were no different. Thus, a single regression was computed using the data of both clutches. I found the following regression line: dry weight (mg) = 0.16 wet weight (mg) - 0.15 ( $n = 86$ ;  $r^2 = 0.96$ ;  $F = 1943.2$ ;  $P = 0.0001$ ).

In this experiment, eggs given as food to hatchlings had a wet weight of  $43.83 \pm 1.12$  mg or a corresponding dry weight of  $6.86 \pm 0.03$  mg. Thus, the mean energy uptake by the consumption of a single egg was 91.3 J.

There was no significant relationship between the wet weight of newly born snails and the dry weight of eggs consumed during the first 4 days of life ( $n = 28$ ;  $r^2 = 0.09$ ;  $F = 2.64$ ;  $P = 0.12$ ).

There was a tendency for a positive relationship between the dry weight of the egg consumed and the wet weight gain of the hatchlings during the 4-day period. The regression (wet weight increase of hatchlings = 0.87 dry weight of egg consumed + 5.37;  $n = 28$ ;  $r^2 = 0.13$ ;  $F = 3.81$ ;  $P = 0.062$ ) showed that the increase in wet weight of egg-predating hatchlings depended on the quantity of eggs consumed during their first 4 days of life. Thus, the degree of egg cannibalism had an influence on the snails' growth.

At the end of the experiment, the shell weight/animal weight ratios were equal in the two groups ( $0.29 \pm 0.01$ ; Mann-Whitney test;  $Z = -0.21$ ;  $P = 0.83$ ). Shell weight represented 29% of the total dry weight of the snail.

A multiple linear regression was calculated using wet weight at an age of 81 days as dependent variable and cumulative food ingestion, wet weight of hatchlings and dry weight of eggs consumed as independent

**Table I.** Calorific values of *Taraxacum officinale* leaves, eggs, faeces and soft bodies of *Helix aspersa*. Mean values  $\pm$  standard errors are given.

Materials	Number of replicates	Ash content (%)	Calorific value (ash-free) $J.mg^{-1}$ dry weight
Snails' eggs	5	$22.48 \pm 1.16$	$17.16 \pm 0.295$
<i>Taraxacum officinale</i> (leaves)	5	$9.28 \pm 1.71$	$17.36 \pm 0.370$
Snails' body			
Cannibalistic snails	2	$5.75 \pm 0.51$	$19.15 \pm 0.287$
Snails' faeces			
Cannibalistic snails	3	$13.25 \pm 2.30$	$21.75 \pm 1.853$
Non-cannibalistic/control snails	3	$10.57 \pm 4.33$	$20.73 \pm 0.603$



variables. Cumulative faeces egestion was not considered, because this variable is highly correlated with cumulative food ingestion ( $n = 22$ ;  $r^2 = 0.72$ ;  $F = 52.45$ ;  $P < 0.001$ ). The cumulative food ingestion was the most important factor explaining 77.6% of the variance. The wet weight of hatchlings and the dry weight of eggs consumed had no significant effect on the live weight at an age of 81 days.

## DISCUSSION

Egg cannibalism is promoted by a low availability of alternative food for hatchlings (Elgar and Crespi, 1992) and food stress is known to increase foraging activity and so the probability of intraspecific contact and predation (Polis, 1981). For these reasons, egg cannibalism occurred in a high percentage of the snails to which an egg was given. In the group of starved snails, the high mortality might be a consequence of the high moving activity (and so mucus and energy expenditures) without finding food. Moreover, like Baur (1994b), I found that small snails were particularly sensitive to starvation even if it was of short duration. Snails which received one egg but did not eat it died much more frequently than the starved controls. In the treatment group (snails that fed on one egg), some snails may have exhibited a lower motivation for food, in relation to their low activity (maybe due to parasitism, weakness or other reasons). Thus, these non-cannibalistic snails are not similar to the control ones; they did not consume the available egg and logically exhibited a higher mortality than the control ones. Like Baur (1994a) in *A arbustorum*, I found no hatching size differences between cannibalistic and non-cannibalistic snails.

The growth and survival benefits of egg cannibalism were important in relation to snails which had not consumed food. The energetic value of eggs (17.2 J/mg) is sim-

ilar to a plant like *Taraxacum*. However, when hatchlings were in the soil, they did not have access to plants; the only food available might be organic matter which is perhaps consumed although it has not been demonstrated (see experimental conditions). The high ash content (22.5%) is probably related to mineral content of snails' eggs. Concerning eggs, our energetic equivalent values were lower than those obtained by Pallant (1974) in the slug *Agriolimax reticulatus* (Müller) but higher than those of Lazaridou-Dimitriadou and Kattoulas (1991) in the snail *Eobania vermiculata* (Müller). In pulmonates, egg capsules are adapted to a terrestrial development and in opposition to Basommatophora, eggs of Stylommatophora possess a mineral shell layer which is particularly rich in calcium carbonate (Bayne, 1968). The zygote is enclosed in albumen and a perivitelline membrane. Egg vitellus in *H aspersa* is rich in amino acids (tryptophan), proteins and glycoproteins (Bayne, 1968; Bole-Richard et al, 1983), carbohydrates (galactogen, glycogen) and calcium (Bayne, 1968). The importance of calcium for the growth of *H aspersa* is well-known (Crowell, 1973) and it is recognized as having an influence on the growth and mortality of juveniles *Achatina fulica* Bowdich (Ireland, 1991). Thus, snails which consumed one egg received nutrients, energy and water.

Adults of *H aspersa* are herbivores. However, proteolytic enzymes are also present in *H pomatia* L and may allow the animals to digest eggs or egg shells during hatching (Purchon, 1968).

Like in other mollusc species, the assimilation of *H aspersa* is high. In this experiment, assimilation efficiency was similar to those recorded by Charrier and Daguzan (1980) and Lamotte and Stern (1987).

The calorific value of the snails' bodies was in agreement with values found for juvenile *H aspersa* (three-month old) by Charrier and Daguzan (1980). The energetic

value of faeces was a little higher than *Taraxacum* calorimetric equivalent. It could be due to mucus content or to concentrations of parts of the food with higher energy (Pallant, 1974). I thought that water content might be higher in faeces than in leaves of *Taraxacum* so that calorific equivalent of 1 mg of fresh leaves would be higher than 1 mg of faeces.

Subsequently, the higher growth rate and lower mortality in cannibalistic snails appeared to be connected to food consumption. The same ingestion, egestion, assimilation rates and assimilation efficiency were found in the two groups. According to their degree of egg-predation, hatchlings ingested more or less energy, nutrients and water. It induced a weight gain during the first 4 days of experiment. Then, because of their greater size at this stage, cannibalistic snails ingested more food and non-cannibalistic and control snails could not compensate for their growth retardation. My results are in agreement with those of Baur (1990b). In the land snail *A. arbustorum*, the cannibalism of eggs induced a higher growth for cannibalistic individuals than for control (fed on lettuce) and a better survival (1.6 times higher). In contrast to my experiment, mortality was low and did not affect snails during the cannibalistic period but later in their growth phase. According to Elmslie (1988), cannibalistic juveniles of *H. aspersa* (on average 1.5 eggs eaten per individual) were more than three times as heavy as those fed on a vegetarian diet. The growth of snails maintained in these conditions is lower than in snails' farms. Food quality (Desbuquois, 1991) and snails' density (Dan and Bailey, 1982; Gomot et al, 1989; Lucarz and Gomot, 1985) are known to influence the growth of *H. aspersa*. In contrast to this experiment, farm snails are fed with a compound food and maintained in group at an optimum density.

It is well-known that there is a considerable growth variation both within a hatch

of mollusc eggs and within a population (Wilbur and Owen, 1964): genetic or environmental differences may explain growth rate differences with an effect on physiological or behavioural characteristics of the individuals. Differences observed in growth rates according to egg cannibalism may partly explain the variability of growth in the offsprings deriving from a single hatch.

Like Elgar and Crespi (1992), potential costs and benefits of oophagy should be discussed. Cannibalism increases growth and induces survival benefits for individuals through nutritional and energetic gains. Egg cannibalism may be a survival mechanism for some individuals in the case of unfavourable conditions. On the other hand, cannibalism may reduce the population size and thus intraspecific competition may decrease. It can be a mechanism of population regulation (Stevens, 1989) and may affect population structure, life-history traits, competition for mates, resources and behaviour (Polis, 1981). The energetic cost of this behaviour is probably very weak because it requires only small movements of the cannibalistic individuals to food access. The animals which exert egg cannibalism do not run any risk because cannibalism on juveniles does not seem to exist and eggs are at a defenceless life stage against predation.

A high growth rate is equally advantageous, because the risk of desiccation decreases when the shell size increases.

According to Lucarz and Gomot (1985), the size at maturity of *H. aspersa* and their growth rate had an influence on their future reproductive activity. On same size individuals of *Cepaea*, reproductive activity is proportional to their growth rates (Oosterhoff, 1977). In *A. arbustorum*, sexual maturity was affected by oophagy although the adult shell size of the snails was not (Baur, 1990b). At the present time, I studied whether egg cannibalism had an influence on the size and age at maturity of *H. aspersa*.

## ACKNOWLEDGMENT

I would like to express my grateful thanks to Dr B Baur and anonymous referees for helpful and valuable advices on an earlier draft of this paper.

## REFERENCES

- Baur B (1988) Egg-species recognition in cannibalistic hatchlings of the land snails *Arianta arbustorum* and *Helix pomatia*. *Experientia* 44, 276-277
- Baur B (1990a) Egg cannibalism in hatchlings of the land snail *Helix pomatia*: nutritional advantage may outweigh lack of kin recognition. *Malacol Rev* 23, 103-105
- Baur B (1990b) Possible benefits of egg cannibalism in the land snail *Arianta arbustorum* L. *Funct Ecol* 4, 679-684
- Baur B (1992) Cannibalism in gastropods. In: *Cannibalism, ecology and evolution among diverse taxa* (MA Elgar and BJ Crespi, eds) Oxford University Press, Oxford, UK, 102-127
- Baur B (1994a) Inter-population differences in propensity for egg-cannibalism in hatchlings of the land snail *Arianta arbustorum*. *Anim Behav* 48, 851-860
- Baur B (1994b) Parental care in terrestrial gastropods. *Experientia* 50, 5-14
- Baur B, Baur A (1986) Proximate factors influencing egg cannibalism in the land snail *Arianta arbustorum* (Pulmonata, Helicidae). *Oecologia Berl* 70, 283-287
- Bayne CJ (1968) Histochemical studies on the egg capsules of eight gastropod molluscs. *Proc Malacol Soc*, London, UK, 38, 199-212
- Bole-Richard MA, Croisille Y, Gomot L, Bride J (1983) Etude électrophorétique comparée des constituants protéiques et glycoprotéiques des œufs et de la glande à albumen au cours du développement et du cycle annuel de l'escargot *Helix aspersa*. *CR Soc Biol* 177, 37-44
- Charrier M, Daguzan J (1980) Consommation alimentaire, production et bilan énergétique chez *Helix aspersa* (Müller) (Gastéropode Pulmoné Terrestre). *Ann Nutr Alim* 34, 147-166
- Crowell HH (1973) Laboratory study of calcium requirements of the brown garden snail, *Helix aspersa* Müller. *Proc Malacol Soc*, London, UK, 40, 491-503
- Dan N, Bailey SER (1982) Growth, mortality and feeding rates of the snail *Helix aspersa* at different population densities in the laboratory, and the depression of activity of helioid snails by other individuals or their mucus. *J Moll Stud* 48, 257-262
- Davies MS, Hawkins SJ, Jones HD (1990) Mucus production and physiological energetics in *Patella vulgata* L. *J Moll Stud* 56, 499-503
- Desbuquois C (1991) Recherches préliminaires sur la nutrition de l'escargot *Helix aspersa* Müller (Mollusque Gastéropode Pulmoné) : importance de la nature de l'aliment, du calcium et d'un complément vitamines-oligo-éléments. Unpublished DEA, university of Rennes, France
- Elgar MA, Crespi BJ (1992) Ecology and evolution of cannibalism. In: *Cannibalism, ecology and evolution among diverse taxa* (MA Elgar and BJ Crespi, eds) Oxford University Press, Oxford, UK, 1-12
- Elmslie IJ (1988) Studies on the feeding of newly hatched *Helix aspersa*. *Snail Farming Res* 2, 45-48
- Gomot A, Gomot L, Boukraa S, Bruckert S (1989) Influence of soil on the growth of the land snail *Helix aspersa*. An experimental study of the absorption route for the stimulating factors. *J Moll Stud* 55, 1-7
- Herzberg F, Herzberg A (1962) Observations on reproduction in *Helix aspersa*. *Am Midl Nat* 68 (2), 297-306
- Ireland MP (1991) The effect of dietary calcium on growth, shell thickness and tissue calcium distribution in the snail *Achatina fulica*. *Comp Biochem Physiol* 98 (1), 111-116
- Lamotte M, Stern G (1987) Les bilans énergétiques chez les Mollusques Pulmonés. *Haliotis* 16, 103-128
- Lazaridou-Dimitriadou M, Kattoulas ME (1991) Energy flux in a natural population of the land snail *Eobania vermiculata* (Müller) (Gastropoda: Pulmonata: Stylommatophora) in Greece. *Can J Zool* 69, 881-891
- Le Calve D (1987) Contribution à l'étude de l'incubation et de son influence sur la croissance des juvéniles chez *Helix aspersa* (Müller) (Mollusque Gastéropode Pulmoné Stylommatophore). *Haliotis* 16, 21-30
- Lucarz A, Gomot L (1985) Influence de la densité de population sur la croissance diamétrale et pondérale de l'escargot *Helix aspersa* Müller dans différentes conditions d'élevage. *J Moll Stud* 51, 105-115
- Mason CF (1970) Food, feeding rates and assimilation in woodland snails. *Oecologia Berl* 4, 358-370
- Oosterhoff LM (1977) Variation in growth rate as an ecological factor in the land snail *Cepaea nemoralis*. *Neth J Zool* 27, 1-132
- Pallant D (1974) Assimilation in the grey field slug, *Agriolimax reticulatus* (Müller). *Proc Malacol Soc*, London, UK, 41, 99-107
- Polis GA (1981) The evolution and dynamics of intraspecific predation. *A Rev Ecol Syst* 12, 225-251
- Purchon RD (1968) Digestion. In: *The Biology of the Mollusca, International Series of Monographs in Pure and Applied Biology, Zoology division*, vol 40 (RD Purchon, ed), Pergamon Press, Oxford, UK, 243-259

- Scherrer B (1984) *Biostatistique*. Gaëtan Morin, Québec, Canada
- Seifert DV, Shutov SV (1981) The consumption of leaf litter by land molluscs. *Pedobiologia* 21, 159-165
- Sokal RR, Rohlf FJ (1981) *Biometry*, 2nd edition, WH Freeman and Company, San Francisco, USA
- Stevens L (1989) The genetics and evolution of cannibalism in flour beetles (genus *Tribolium*). *Evolution* 43 (1), 169-179
- Wilbur KM, Owen G (1964) Growth. In: *Physiology of Mollusca*. Vol I (KM Wilbur and CM Yonge, eds). Academic Press, London, UK, 211-242
- Zar JH (1984) *Biostatistical analysis*. 2nd ed, Prentice-Hall International, New York, USA